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Predicting seasonal patterns of California cetacean density based on remotely sensed
environmental data

A Dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Marine Science

by
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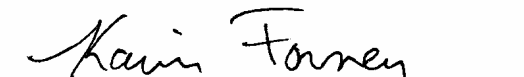
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July 2007

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DEDICATION

To John,

with love

But now ask the beasts, and let them teach you;
And the birds of the heavens, and let them tell you.
Or speak to the earth, and let it teach you;
And let the fish of the sea declare to you.

Job 12: 7-8

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ABSTRACT

Predicting seasonal patterns of California cetacean density based on remotely sensed environmental data

by

Elizabeth Ann Becker

Temporal and spatial variability in species distribution and abundance is a major source of uncertainty in ecological research and marine resource management. This is particularly important in dynamic systems like the California Current, a region defined by high variability at multiple temporal and spatial scales. This dissertation focuses on the quantitative analysis of the seasonal distribution patterns of California cetaceans. Chapter One provides an introduction to the study area, the research questions, and the analytical methods. In Chapter Two, I reanalyzed aerial survey data collected in central and northern California from 1980 to 1983 using more recent, advanced line-transect methods to estimate cetacean densities. The revised estimates allowed for a quantitative examination of seasonal and interannual patterns of cetacean abundance for 1980-83, and a statistical comparison of spring abundance between the early 1980s and the 1990s. While significant inter-decadal differences in spring abundance were evident for only one of the five species analyzed, the revised 1980-83 abundance estimates reveal variability in both

seasonal and interannual patterns for the majority of species considered. In Chapter Three I developed generalized linear and generalized additive models to predict encounter rate, group size, and density for 10 cetacean species based on static and dynamic environmental variables. Sighting data used for modeling were collected off California during four summer/fall surveys between 1991 and 2001. I evaluated the predictive ability of models based on various temporal and spatial resolutions of remotely sensed sea surface temperature, and compared the performance of models built with remotely sensed vs. *in situ* environmental data. Results indicate that, when sample size is sufficient, cetacean-habitat models developed using fairly coarse-scale satellite data have predictive ability that meets or exceeds models developed with analogous *in situ* data. In Chapter Four I examined whether models built with data collected in the summer can be used in association with winter remotely sensed data to predict distribution patterns across seasons. This approach inherently assumes that the range of interannual environmental variability overlaps that of seasonal environmental variability in the study region. Changes in seasonal distribution patterns were captured effectively for three of the five species evaluated.

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LIST OF ACRONYMS

AIC	Akaike's Information Criterion
ASL	above sea level
ASPE	average squared prediction error
AVHRR	Advanced Very High Resolution Radiometer
BCa	bias-corrected and accelerated
BLM	Bureau of Land Management
CalCOFI	California Cooperative Oceanic Fisheries Investigations
CDAS	Computer Database Analysis System
CI	confidence interval
CV	coefficient of variation
ENSO	El Niño Southern Oscillation
ESW	effective strip width
GAM	generalized additive model
GIS	geographic information system
GLM	generalized linear model
GMT	Generic Mapping Tool
GOF	goodness-of-fit
GPS	global positioning system
K-S	Kolmogorov-Smirnov
LORAN	Long Range Navigation
MMPA	Marine Mammal Protection Act
MMS	Minerals Management Service
nmi	Nautical miles
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
OPeNDAP	Open-source Project for a Network Data Access Protocol
PFEL	Pacific Fisheries Environmental Laboratory
SCB	Southern California Bight
SE	standard error
SERDP	Strategic Environmental Research and Development Program
SST	sea surface temperature
SWFSC	Southwest Fisheries Science Center
VLF	very low frequency

CHAPTER ONE

INTRODUCTION AND BACKGROUND

by

Elizabeth A. Becker

Introduction

Ecology is the study of the distribution and abundance of organisms and how they relate to one another and their environment. A fundamental goal of marine ecology is to understand the factors that determine the distribution patterns of marine species. This presents unique challenges due to the dynamic nature of marine ecosystems (Mann and Lazier 2006). Understanding how the environment affects species abundance and distribution also has practical management applications. We need to understand the mechanisms determining marine species distributions in order to mitigate potential anthropogenic impacts. Temporal and spatial variability in species distribution and abundance remains a major source of uncertainty in managing marine resources (Ralls and Taylor 2000). This is particularly important in dynamic systems like the California Current, a region defined by high variability at multiple temporal and spatial scales (Hickey 1998).

This dissertation focuses on the quantitative analysis of the seasonal distribution patterns of California cetaceans. The following subsections describe

pertinent aspects of the study region, provide background information on the motivation for this research, and summarize information on the methods used and key studies leading up to this research. In addition, a summary of the following chapters is provided. This research has both ecological and management applications. In addition, the results provide insight into modeling techniques that are applicable to other apex marine predators.

Study Area

The California Current is the eastern limb of the North Pacific gyre, the major anticyclonic gyre in the northern hemisphere (Figure 1.1). The California Current is a near-surface (0-500 m), equatorward flow characterized by low temperatures, low salinities, and high dissolved oxygen levels originating from Pacific subarctic waters (Lynn and Simpson 1987). The California Current extends from the continental shelf break to approximately 1,000 km off the California coast (Hickey 1998). Except near the coast, the California Current carries water equatorward throughout the year. Similar to other eastern boundary current systems, the California Current System is characterized by episodic upwelling events and corresponding high levels of primary productivity. Increased primary productivity can be transferred via the food web to apex predators such as cetaceans (Ryther 1969). During spring and early summer, the prevailing winds along the North American coast are north-northwesterly, giving rise to upwelling events that bring relatively cold, saline, nutrient-rich, oxygen-deficient waters from depth to the

surface. The driving force for these surface winds is the strength of the gradient between the continental thermal low over California and the North Pacific high-pressure system (Hickey 1979, 1998). The study area for this dissertation encompasses approximately 818,000 km², extending from the California coast to about 556 km (300 nmi) offshore (Figure 1.2).

The California Current System comprises several surface and subsurface currents that form dynamic relationships, contributing to seasonal and larger-scale variations in transport, upwelling patterns, and water characteristics (Hickey 1979, 1998). The poleward and equatorward flows included in this system are generally characterized as large-scale (> 500 km alongshore) currents. Typically the California Current refers to the equatorward flow, the California Undercurrent refers to the poleward subsurface flow over the continental slope, and the Davidson Countercurrent (north of Point Conception) refers to a coastal poleward current (Pares-Sierra and O'Brien 1989). South of Point Conception there is also an inshore surface flow typically called the Southern California Eddy during periods when the flow recirculates within the Southern California Bight (SCB) and the Southern California Countercurrent when the flow travels around Point Conception. In this region, where there is an abrupt change in the angle of the coastline (Figure 1.2), circulation patterns and forcing mechanisms differ significantly from other areas on the U.S. West Coast (Hickey 1993; Winant et al. 2003; Dever 2004). Surface circulation in the Santa Barbara Channel is particularly complex, exhibiting flow fluctuations at various spatial and temporal scales (Hendershott and Winant 1996;

Harms and Winant 1998). Since 1950, large-scale hydrographic sampling of the California Current System has been conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI), providing many of the data used to gain our current understanding of this dynamic system (e.g., Chelton et al. 1982; Hayward and Venrick 1998; Bograd and Lynn 2003) .

Environmental variability in the study area

The California Current System contains four different water masses, each defined by its temperature, salinity, nutrients, and dissolved oxygen at the time it enters the system. In addition to upwelled water (generally relatively cold, saline, nutrient-rich, and oxygen-poor), the California Current System contains water that originated in the Pacific subarctic (low temperature, low salinity, high dissolved oxygen), the eastern central North Pacific (warm, saline, depleted nutrients, low dissolved oxygen), and the northeastern tropical Pacific (high temperature, high salinity, high nutrients, low dissolved oxygen) (Lynn and Simpson 1987). Seasonal variations in water mass characteristics are determined by changes in transport and vertical adjustments in the density field, largely related to the seasonal migration of the North Pacific high-pressure system. Seasonal and interannual variations in water mass characteristics and biological productivity have been documented (Roemmich and McGowan 1995).

The structure of the California Current System and closely associated upwelling patterns is sensitive not only to seasonal and interannual changes but also

to longer-term climatic oscillations such as El Niño-Southern Oscillation (ENSO) events. An ENSO event represents a disruption in the ocean-atmosphere system that results in the development of abnormally warm sea surface temperatures (SSTs) across the eastern tropical Pacific (Cane 1983; Fiedler et al. 1992). Many studies have documented the severe reduction of primary productivity in the coastal northeastern Pacific as a result of ENSO events, resulting in part from a decrease in the quantity of limiting nutrients transported to the surface waters due to depression of the thermocline (Barber and Chavez 1983; Cane 1983; Fiedler et al. 1992; Kudela and Chavez 2002).

In addition to documented declines in primary productivity associated with ENSO events, changes in the abundance and distribution of zooplankton, benthic invertebrates, fish, sea turtles, and seabirds have also been observed (Barber and Chavez 1983; Pearcy and Schoener 1987). While population reductions are evident in many cases, other studies reveal considerable shifts in species distributions. For example, during the very strong 1982-83 ENSO event, the ranges of many species extended northward into the mid-latitudes of the northeastern Pacific (Percy and Schoener 1987). Because cetaceans are highly mobile, it is expected that an ENSO event would result in changes in local abundance and distribution patterns in response to the change in oceanographic conditions and the availability of prey.

The opposite extreme of the Southern Oscillation cycle (i.e., a “La Niña” event) is generally characterized by cooler than average SSTs and high levels of sustained coastal upwelling off California (Schwing et al. 2000). The oscillation

between El Niño and La Niña events is highly irregular but generally occurs every 3 to 7 years.

Multidecadal fluctuations have been shown to have basin-wide ecosystem effects similar to El Niño and La Niña but on a longer time scale (Chavez et al. 2003). The term Pacific Decadal Oscillation (PDO) is used to describe climate variability and ecosystem effects in the north Pacific that vary on time scales of 20 to 30 years (Mantua et al. 1997). A “regime shift” describes the rapid change between an eastern Pacific cool phase and a warm phase. Regime shifts have been associated with major ecosystem changes in the California Current System, including changes in upper-ocean temperatures, upwelling strength, zooplankton biomass, fish recruitment, and salmon catch (Hare and Mantua 2000; McGowan et al. 2003).

Research and management implications

Environmental variability is evident in the California Current System at seasonal, interannual, ENSO, and decadal scales. Environmental variability is increasingly recognized as an important source of uncertainty in marine stock assessment research and ecological studies concerning broad taxonomic groups including invertebrates, fish, seabirds, and marine mammals. For example, decadal shifts in sardine and anchovy abundance have been linked to oceanographic variability in eastern boundary current regions (MacCall 1996; Chavez et al. 2003). Recently, numerous studies have attempted to identify relationships between commercially valuable marine species and environmental parameters to improve our

understanding of observed variation in interannual recruitment, year-class abundance, and longer-term population fluctuations (e.g., Pyper and Peterman 1999; Maravelias et al. 2000; Rosenkranz et al. 2001; Koslow et al. 2002; Chavez et al. 2003). Protected marine species, such as seabirds, marine mammals, sea turtles, and certain highly migratory fish, are also fundamentally affected by environmental variability, although the mechanisms by which this happens depend on each species' life history.

For short-lived species and species with high fecundity, environmental variability can have profound effects on population dynamics by influencing birth and death processes. Such biological effects are well known for ENSO events (e.g., Barber and Chavez 1983; Trillmich and Limberger 1985). In contrast, long-lived, highly migratory species often respond to oceanographic variability by moving over large geographical distances to locate suitable habitats, rather than (or in addition to) responding through changes in survival and reproductive success (Ainley et al. 1995a, b; Pyle et al. 1996; Forney and Barlow 1998; Sydeman and Allen 1999; Tynan 1999; Forney 2000; Benson et al. 2002). Nevertheless, in the case of both population declines and geographic movement, the net effect for all marine species is an increase in the variability of measures used for stock assessment purposes (abundance, density, catch per unit effort, etc.) and a correspondingly low statistical power to detect trends (Gerrodette 1987; Peterman and Bradford 1987; Forney et al. 1991; Edwards and Perkins 1992; Taylor and Gerrodette 1993; Forney 1999). For example, Forney (2000) suggested that dramatic differences in the abundance

estimates of some California cetacean species were due to movement of the animals in and out of the study area in response to changing oceanographic conditions rather than actual population declines. Abundance estimates for fixed geographic regions (e.g., California) may thus be based on a different proportion of the population in each year, introducing considerable variability into abundance time series, and causing uncertainty in marine stock assessments and ecological studies.

For most cetacean species, abundance is estimated using line transect methods without allowance for direct measures of environmental variability (Burnham et al. 1980; Buckland et al. 2001). Recently, however, there has been increased recognition that incorporation of environmental variables can improve conventional estimation methods (Hedley et al. 1999; Forney 2000; Hedley and Buckland 2004; Ferguson et al. 2006; Gomez de Segura 2007). Further, abundance estimates that incorporate oceanographic variability can improve trend analyses and increase the accuracy of stock assessments (Forney 1999, 2000). Predictive cetacean-habitat models that incorporate oceanographic variability can improve our ability to identify cetacean distribution patterns at various spatial resolutions (Ferguson et al. 2006). The need for effective predictive models of cetacean occurrence and distribution has become critical for marine resource managers who must select minimal-impact locations or seasons for an increasing number of human activities with potential to harm cetaceans (e.g., Navy test and training activities, seismic surveys, fisheries interactions, etc.). In addition to management implications, understanding the causes and consequences of changes in the

abundance and distribution of populations is a fundamental goal of ecology and conservation biology.

In order to assess the effects of oceanographic variability on cetacean abundance and distribution, environmental measures must be readily obtainable, ideally on a synoptic and repetitive basis, over broad ocean areas. In addition, it is important to have access to data collected across years and seasons, in order to capture the range of seasonal and interannual environmental variability. Shipboard surveys provide the most comprehensive species and oceanographic data, and the majority of modeling efforts concerning cetacean-environment relationships have used measures of oceanographic conditions collected from ships. A disadvantage of shipboard surveys is that they are expensive and time-consuming, so usually do not allow for repetitive surveys of large areas. Off the California coast, the abundance of cetaceans has been estimated from 1991-2001 shipboard line-transect surveys conducted during the summer and fall (Barlow 2003). Rough weather conditions make it difficult to collect shipboard line-transect data in winter and spring. Many of the data that exist for these seasons have been collected during aerial surveys, which typically do not include the collection of complementary *in situ* oceanographic data. In this case, remote sensing can provide a comprehensive source of environmental data.

Cetacean-habitat Modeling Techniques

Redfern et al. (2006) provide a review of cetacean-habitat modeling techniques, including topics such as the motivation for developing cetacean-habitat models, the importance of spatial and temporal scale, cetacean and environmental data collection procedures, and statistical modeling techniques. Many of the statistical procedures now used for predictive habitat modeling evolved with the increased speed and power of computers; complex calculations are now commonly performed using computer-intensive methods in statistics (Diaconis and Efron 1983; Efron and Tibshirani 1991).

Generalized linear and generalized additive models

There has been a recent increase in the development of species-habitat distribution models using data collected from systematic surveys of cetaceans, as well as opportunistic sighting and historic whaling data. Generalized linear models (GLMs; McCullagh and Nelder 1989) based on logistic regression have been used to relate cetacean presence/absence to environmental and geographic variables (Moses and Finn 1997; Waring et al. 2001; Davis et al. 2002; Baumgartner et al. 2003; Hamazaki 2002; Yen et al. 2004; Tynan et al. 2005). Another form of GLM, Poisson regression, also has been used to relate the locations of cetacean groups to environmental data (Gregs and Trites 2001; Cañadas et al. 2002). Analytical methods for producing density estimates from GLMs have been described (Hedley

and Buckland 2004), but to date no other studies have used GLMs to estimate absolute density or abundance.

Although GLMs are still commonly used, there is a growing recognition that variability in species abundance might best be explained by nonparametric relationships with habitat gradients (Austin 2002; Oksanen and Minchin 2002), and there is growing acceptance of the use of generalized additive models (GAMs; Hastie and Tibshirani 1990) to quantitatively explore relationships between cetaceans and environmental variables. Hedley et al. (1999) described analytical methods for applying GAMs to cetacean-habitat data collected from strip- and line-transect surveys. Forney (2000) used GAMs to relate cetacean encounter rates to environmental variables, and demonstrated that GAMs represent an effective tool for reducing uncertainty caused by environmental variability. Results from this research also show, however, that models are only effective if the data they are based on capture a wide range of oceanographic variability. For this reason, models should be constructed with multi-year data and cross-validation methods.

Both Hedley et al. (1999) and Forney (2000) used cetacean group encounters as response variables in the models and did not incorporate potential variability in the size of the groups. Group size is an important factor in estimating cetacean density, particularly for those species known to occur in highly variable group sizes (Buckland et al. 2001). Hedley and Buckland (2004) described methods for creating spatial models of group size in order to estimate population density. Ferguson et al. (2006) developed separate encounter rate and group size GAMs to produce density

estimates for cetaceans in the eastern tropical Pacific. Cetacean abundance estimates derived from GAMs were used in a study that compared estimates from the spatial models to those made using standard line-transect methods (Gomez de Segura et al. 2007).

The GAM-based framework is the current benchmark method for modeling cetacean density. However, GAMs have been criticized for being difficult to interpret ecologically (Olivier and Wotherspoon 2005). Further, there is a lack of comparative studies evaluating results of two or more statistical methods applied to the same data set (Guisan and Zimmermann 2000; Wilfried et al. 2003). The majority of ecological studies that provide a direct comparison of GLMs and GAMs are found in the field of vegetation science (e.g., Franklin 1998; Wilfried et al. 2003). For this dissertation I developed both GLMs and GAMs to model the relationship between cetacean sighting data and oceanographic data, building on the modeling framework developed by Ferguson et al. (2006). Results of the two approaches are compared.

Models using remotely sensed oceanographic data

Using remotely sensed data to study the distribution patterns of cetaceans is not a new idea. More than 25 years ago, a conference was held in Santa Barbara, California, to address the use of remote sensing for studying and managing marine mammals (Botkin et al. 1981). Scientists from the United States and England spent two days discussing 1) available techniques for using remote sensing to study marine

mammals, 2) why available techniques had not been fully utilized, 3) the role of marine mammals in marine systems, 4) why understanding their distribution patterns is significant from an ecological perspective, and 5) how remote sensing might contribute to their management and conservation. The use of remotely sensed environmental measures in cetacean-habitat studies has increased during the last 25 years, although in many studies satellite-derived data have been used as supplements to *in situ* data or when equipment failure precluded the collection of along-track data (e.g., Davis et al. 1998, 2002; Baumgartner et al. 2001; Hamazaki 2002).

Smith et al. (1986) suggested that satellite-derived measures of oceanographic parameters provide data useful in identifying distinct oceanic habitats, interpreting observed distribution patterns of cetaceans, and estimating their abundance. They emphasized that the synoptic nature of remotely sensed data is important for cetacean-habitat studies because it provides information on the scale and dynamics of physical and biological features characterizing the marine environment. In addition, these data can be used to optimize survey efforts and statistically investigate associations between cetaceans and environmental variables. Remotely sensed data have been used in cetacean-environment studies to characterize conditions throughout specific study areas. For example, remotely sensed measures of both SST and chlorophyll *a* concentration were used to identify productive regions in the Ligurian Sea to enable a qualitative correlation of marine mammals to physical and biological parameters (D'Amico et al. 2003). Remotely sensed SST data were used to identify the locations of warm core rings in the North

Atlantic in order to determine whether sperm whale sightings were significantly associated with these features (Waring et al. 1993; Griffin 1999). Davis et al. (2002) used dynamic height derived from satellite sea surface altimetry data to direct the survey ship during data collection efforts as well as retrospectively to evaluate the association of cetacean sightings and hydrographic features.

Remotely sensed data also have been used to investigate potential habitat associations in the absence of *in situ* oceanographic data, often in association with aerial survey data or in conjunction with historic whaling records. Brown and Winn (1989) used satellite-derived SST data to investigate distribution patterns of right whales based on sightings from aerial surveys in the Atlantic. Jaquet et al. (1996) evaluated the distribution of sperm whales based on 19th century whaling records relative to contemporary satellite-derived ocean color measurements averaged over an 8-year period (1978-1986). The pigment data were used to represent variability in production of the temperate and tropical Pacific Ocean. Monthly mean SST anomalies estimated from satellite, buoy, and shipboard measurements were used to examine trends in harbor porpoise abundance as indicated by sightings during aerial surveys conducted off central California (Forney 1999). Satellite-derived measures of SST and chlorophyll *a* concentration were used in conjunction with blue whale call rates in the northwest Pacific to investigate potential habitat associations (Moore et al. 2002). In addition to monthly averaged SST and chlorophyll *a* values, they investigated blue whale associations with frontal regions, which they defined by sharp SST gradients.

Objectives of this Dissertation

Quantitative analyses of species-environment associations are one of the main ways to study species ecology (Johnson 1980). The research goals for this dissertation are to 1) provide a quantitative examination of seasonal, interannual and interdecadal trends in the abundance and distribution of several California cetacean species; 2) develop and evaluate techniques for including remotely sensed environmental data into species-environment models and identify the most effective temporal and spatial resolutions for such modeling and assessment work; 3) compare the predictive ability of cetacean-habitat models built with remotely sensed and *in situ* oceanographic data; and 4) assess whether species-environment models developed using remotely sensed environmental data are able to predict species densities across seasons in the California Current, where the range of interannual variability can overlap the range of seasonal variability. This research will provide a foundation for future research aimed at developing robust seasonal models of marine mammal distribution using remotely sensed environmental data.

Active areas of current research in this field include developing cetacean prey indices to use as predictor variables in cetacean-habitat models (Vilchis and Ballance 2005), investigating the appropriate scale for modeling (Redfern et al. *in review*), and evaluating methods for estimating variance (Ferguson and Barlow *in prep*). Future work should focus on developing satellite-derived products that improve the predictive performance of cetacean-habitat models, such as water mass proxies. In

addition, future analyses should focus on increasing our ecological understanding of cetacean prey distributions, and using this knowledge to develop more effective proxy measures from satellite-derived data. Such variables may lead to advances in predictive modeling and provide further insight into the ecological relationships between cetaceans and their environment.

Overview of Chapters Two through Four

The remaining chapters of this dissertation each contribute to the examination of seasonal distribution patterns of California cetacean density, with emphasis on the development of predictive habitat models that incorporate remotely sensed environmental data. The goal of Chapter Two, “Seasonal and decadal patterns of cetacean abundance off central and northern California based on 1980-83 and 1991-92 aerial surveys,” is to increase our knowledge of cetacean variability at seasonal, interannual, and decadal time scales. Aerial survey data collected in central and northern California from 1980 to 1983 during all seasons were reanalyzed using more recent, advanced line-transect methods to estimate cetacean densities. Re-analysis of the large 1980-83 dataset eliminated or reduced several sources of bias present in the original analysis, resulting in revised, more accurate density and abundance estimates of cetaceans for this time period. The revised density estimates and associated measures of uncertainty allowed for a quantitative examination of seasonal and interannual patterns of abundance for 1980-83. In addition, the revised estimates allowed for the first statistical comparison of cetacean

abundance between the early 1980s and the 1990s. While significant inter-decadal differences in spring abundance were evident for only one of the five species analyzed, the revised 1980-83 abundance estimates reveal variability in both seasonal and interannual patterns for the majority of species considered. Results from this study provide additional evidence that interannual variability for many California species can be as high as, or greater than, seasonal variability. The 1980-83 data sets now can be used for future quantitative analyses, including the development of species-environmental models using remotely sensed data.

Because the collection of *in situ* data during surveys is expensive and not always possible, Chapter Three, “A comparison of California Current cetacean-habitat models developed using *in situ* and remotely sensed sea surface temperature data,” provides a comparison of models built with remotely sensed data to those built with analogous *in situ* data. This chapter describes the methodology used to develop and evaluate generalized linear and generalized additive models of encounter rate and group size for 10 cetacean species, as well as the process for estimating their population density. To examine whether remotely sensed data can be used more broadly, and at what scales, this chapter also includes an evaluation of the predictive ability of models based on various temporal and spatial resolutions of remotely sensed SST. Models were evaluated by comparing model-based predicted density estimates to those estimated directly from the survey data, as well as their ability to identify species-environment relationships that are consistent with known distribution patterns. Results indicate that, when sample size is sufficient (ideally

greater than 100 sightings), cetacean-habitat models developed using fairly coarse-scale satellite data have predictive ability that meets or exceeds models developed with analogous *in situ* data. In addition, satellite-derived estimates of variance in sea surface temperature were found to be more effective at characterizing frontal activity due to their ability to measure heterogeneity in two dimensions. The predictive ability of cetacean-environment models was found to be affected by the level of complexity of the oceanographic environment; more data were required to parameterize models for species that inhabit diverse environments. In the California study area, persistent cloud cover is often associated with coastal upwelling areas in summer. Ironically, in these dynamic areas where more data are needed for modeling, cloud cover often limits the amount of passive infrared remotely sensed SST data that are available. SST data obtained from rapidly-sampling geostationary infrared sensors and from microwave radiometers could help prevent data loss due to cloud cover. Such datasets should be evaluated in future studies.

Chapter Four, “Predicting seasonal densities of California cetaceans based on models built with remotely sensed environmental variables,” expands on the findings of Chapter Three, and examines whether models built with data collected in the summer can be used in association with winter remotely sensed data to predict distribution patterns across seasons. Models developed using shipboard survey data collected in summer during several different years (1991, 1993, 1996, 2001) were used to predict cetacean density in winter based on environmental conditions measured in winter by remote sensing. This approach inherently assumes that the

range of interannual environmental variability overlaps that of seasonal environmental variability in the study region. Models built with remotely sensed data offer a potential means of estimating density for seasons when cetacean surveys are difficult to conduct due to weather (e.g., winter in the California Current). This approach, if proven effective, would improve our ability to mitigate anthropogenic impacts and understand cetacean ecology during times when survey data are more limited. Predictions of density in winter based on the summer models were compared to estimates derived from aerial survey data collected during winter 1991 and 1992, as well as to those of a null model (i.e., density estimates derived from summer shipboard surveys without consideration of environmental data). Results were examined in light of known cetacean distribution patterns documented from previous California cetacean-habitat studies. Results indicate that, for some species present off California year-round, models based on four summer/fall seasons with cetacean and environmental data had some ability to predict seasonal distribution of cetaceans in winter/spring. However, additional data are needed to improve predictive performance. When predicting across seasons, geographic patterns of species density were captured for three of the five species considered. More data collected over a range of oceanographic conditions are needed to make the models robust and improve predictive performance.

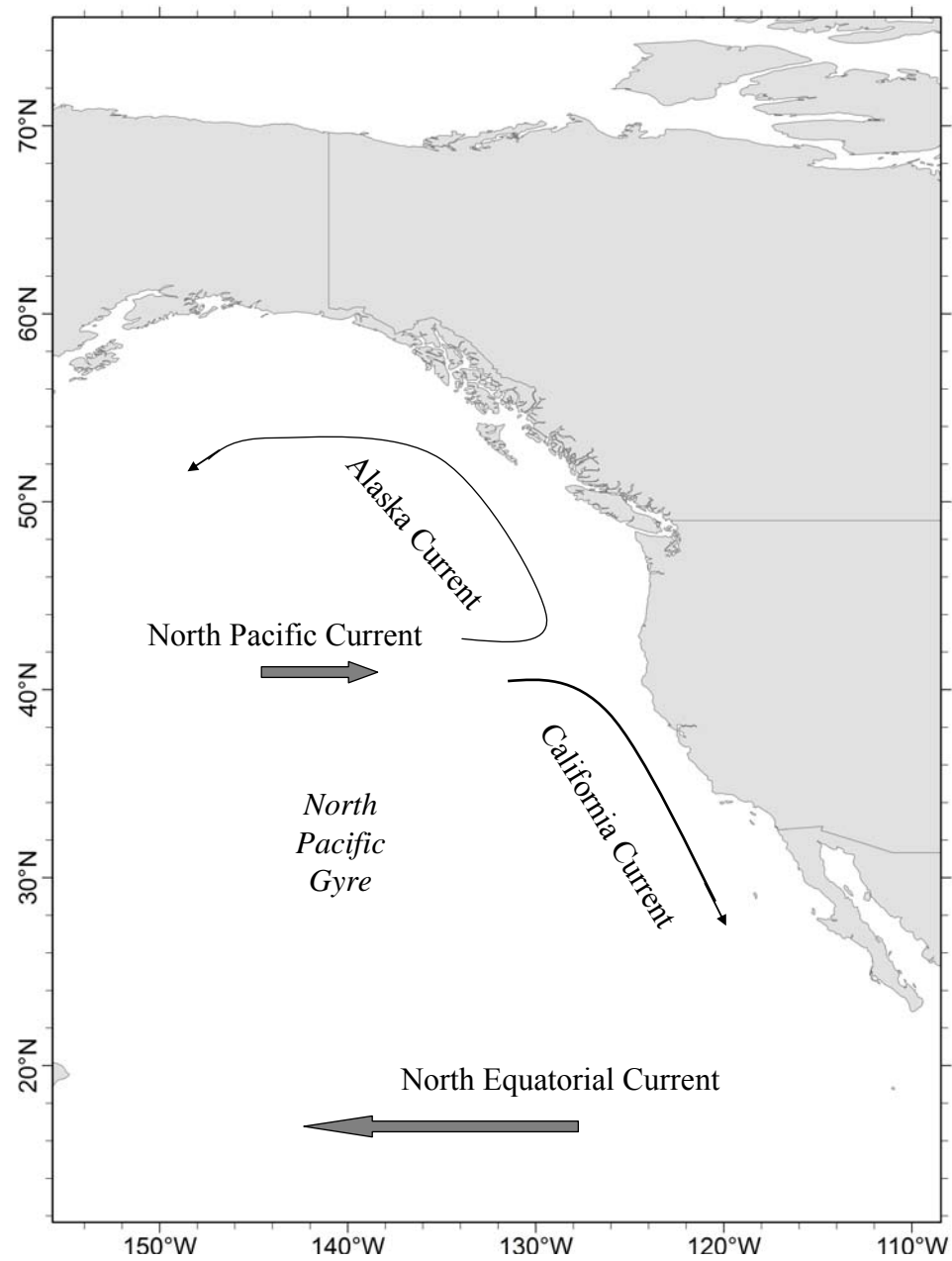


Figure 1.1. Major surface currents of the northeast Pacific Ocean.

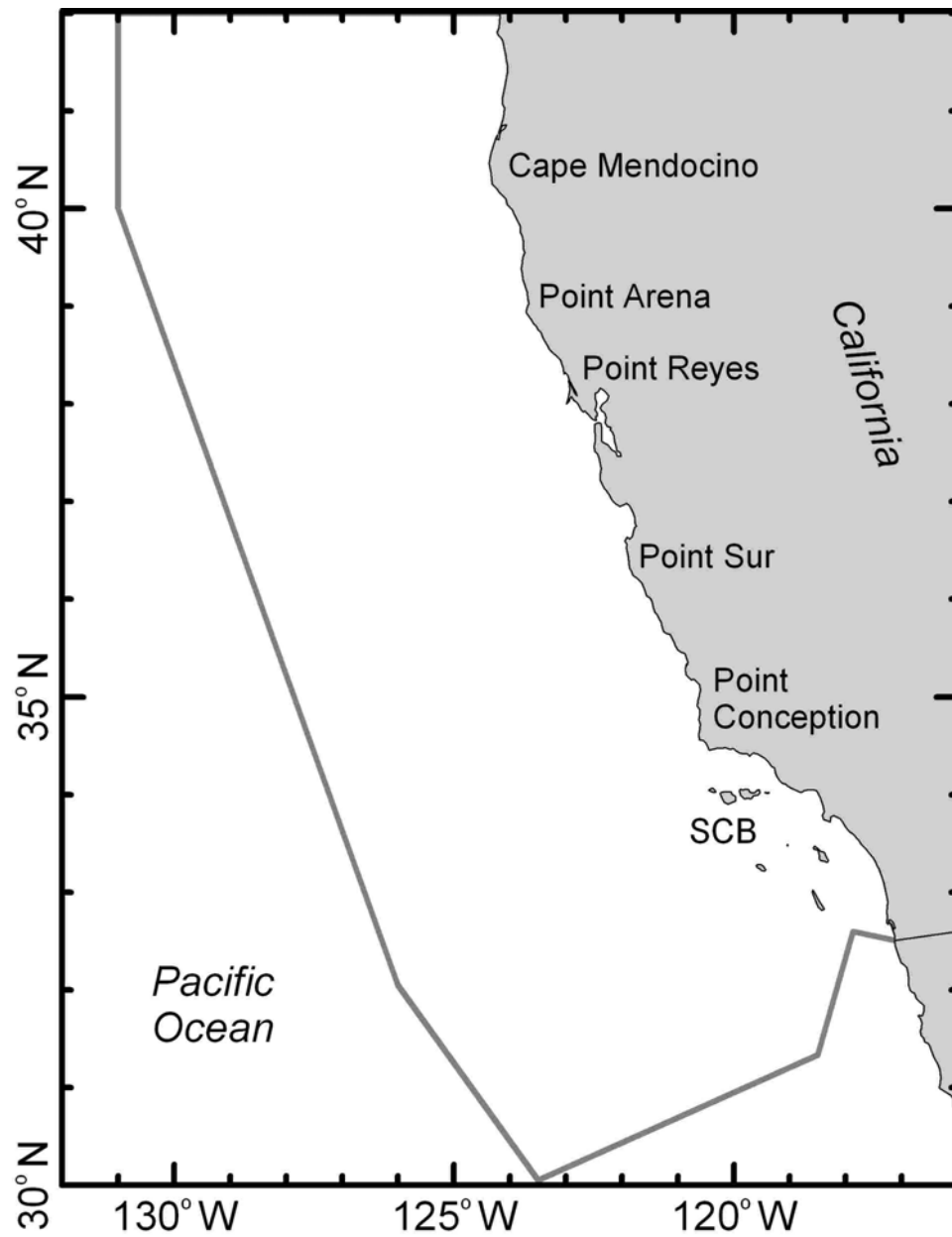


Figure 1.2. Study area off the California coast. The light gray line depicts the outer boundary of the study area, which encompasses approximately 818,000 km². SCB = Southern California Bight. One degree of latitude = 111 km.

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CHAPTER TWO

SEASONAL AND DECADAL PATTERNS OF CETACEAN ABUNDANCE OFF CENTRAL AND NORTHERN CALIFORNIA BASED ON 1980-83 AND 1991-92 AERIAL SURVEYS

by

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Abstract

Aerial line-transect data collected monthly off central and northern California from March 1980 to February 1983 provide one of the most comprehensive sources of cetacean sighting data for this region. However, variances reported for the original density estimates were incomplete, preventing statistical comparisons to more recent density estimates and among the seasons surveyed. In this study, we reprocessed and reanalyzed data collected from the high-altitude (300 m above sea level) 1980-83 surveys using more recent, advanced analysis techniques, including estimates of precision. The re-analysis eliminated or reduced several sources of bias present in the original analysis, resulting in revised 1980-83 estimates of cetacean density and abundance in the approximate 125,100 km² study area. Seasonal and interannual patterns of abundance were examined quantitatively. All revised density

and abundance estimates were lower than the original estimates derived from the survey data. The revised abundance estimates for five of the most common species were statistically compared to more recent aircraft-based estimates for spring (February-April) 1991-92 using a confidence-interval based bootstrap technique. No significant inter-decadal differences in spring abundance were identified for Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), or humpback whale (*Megaptera novaeangliae*). The abundance of Dall's porpoise (*Phocoenoides dalli*) inshore of the 2,000-m isobath was found to be significantly lower in 1980-83 than 1991-92. Seasonal and interannual variability in abundance were evident for all five of these species.

Introduction

Relative to many other areas of the world's oceans, waters off California have been surveyed extensively for cetaceans. Systematic line-transect surveys have been conducted periodically off the California coast since 1975 for the purpose of estimating cetacean population numbers and distribution patterns (Dohl et al. 1978, 1986; Lee 1994). The 1994 amendments to the Marine Mammal Protection Act (MMPA) require the National Marine Fisheries Service (NMFS) to produce stock assessment reports for all cetaceans in U.S. waters. The first stock assessment report that included estimates of numbers of cetaceans occurring off California was published in 1995 (Barlow et al. 1995), and the NMFS Southwest Fisheries Science

Center (SWFSC) periodically conducts aerial and shipboard cetacean surveys off California to obtain updated estimates of abundance. A few studies have examined historical and seasonal changes in the abundance of cetaceans off California (Barlow 1993; Forney and Barlow 1998), but the available data for such analyses are limited, particularly compared to other marine species such as zooplankton and fish, for which data have been collected routinely off California for more than 50 years (Hare and Mantua 2000; McGowan et al. 2003).

By far the most extensive line-transect survey effort off California was conducted from 1980 to 1983 off central and northern California for the Bureau of Land Management's Outer Continental Shelf office (now the Minerals Management Service [MMS]). Monthly surveys were conducted from fixed-wing aircraft at both high and low altitude (1,000 ft and 200 ft above sea level [ASL], respectively), covering a study area from Point Conception to the Oregon border and offshore out to 90 nautical miles (nmi). Preliminary cetacean density and abundance estimates derived from these survey data were reported by Dohl et al. (1983); however, the methodology used for analysis was not comparable to more recent, advanced analysis techniques, and platform-specific biases were not taken into account. Aircraft used for recent SWFSC surveys were equipped with viewing ports placed in the plane's belly to provide one observer with an unobstructed view of the trackline. In addition, bubble windows were placed on the left and right sides of the aircraft to allow observers to look directly beneath as well as to the sides of the plane. In contrast, the MMS aerial surveys were conducted in a plane with flat side windows

and no belly windows. The search pattern, and therefore the proportion of cetaceans detected, is different for these two aircraft configurations. Furthermore, Dohl et al. (1983) did not provide estimates of variance for the majority of the abundance estimates and the confidence intervals that were provided did not include variance associated with group size estimation. Therefore, direct comparisons between Dohl et al.'s (1983) abundance estimates and those derived from recent survey data would not provide an accurate account of population changes over time.

Factors such as Beaufort sea state and group size affect the detectability of cetaceans and need to be accounted for when estimating abundance (Barlow et al. 2001). Stratification or covariates have been used to improve precision and reduce the bias of abundance calculations in such cases (Barlow 1995, 2006; Forney et al. 1995; Forney and Barlow 1998; Carretta et al. 2001). The addition of belly windows in survey aircraft has also allowed for a conditionally independent survey design (Barlow 1995; Forney et al. 1995) that enables estimating the proportion of cetaceans at the surface near the trackline that are missed, i.e., perception bias (Marsh and Sinclair 1989). Prior to 1991, conditionally independent observers were not used on aerial surveys off California (Lee 1994). For some species, correction factors also have been developed to account for availability bias associated with animals near the trackline and missed because they are diving at the time the survey platform passes by. The latter correction factor can be derived through multi-platform experiments (Laake et al. 1997) or calculated based on a species' surfacing

and diving behavior relative to the speed of the survey platform and search pattern of observers (Barlow 1995).

Dohl et al. (1983) estimated lateral detection functions as part of their original analysis, but estimates apparently were not stratified by group size or sea state (M. Bonnell, pers. comm. 1997), and no correction factors were applied to account for animals missed on the trackline due to either perception or availability bias. In the absence of other biases, this would have led to the underestimation of abundance for most species, particularly those that are more difficult to detect (e.g., Dall's porpoise, *Phocoenoides dalli*) and those known to dive for long periods (e.g., sperm whale, *Physeter macrocephalus*). However, other sources of bias do exist, as demonstrated below, and the overall accuracy of the Dohl et al. (1983) estimates is difficult to evaluate.

Some of the methodological limitations in the 1980-83 results as originally reported could be resolved in whole or in part by re-analysis via updated procedures. Such a re-analysis was considered well justified given the unmatched comprehensiveness of the 1980-83 survey and its potential value as a basis for comparison with more recent studies. In this paper, we have reanalyzed the MMS high-altitude survey data for central and northern California to provide more accurate 1980-83 abundance estimates and to enable a quantitative comparison to abundance estimates from more recent surveys. We selected the high-altitude survey data because that survey was designed specifically to survey cetaceans and the data collection methods were most similar to recent methodology. Although cetacean

sightings were recorded during the MMS low-altitude surveys, they were focused primarily on seabirds, pinnipeds, and sea otters. In addition, during the low-altitude surveys observers searched on only one side of the aircraft. For comparison we selected the SWFSC 1991-92 California coast aerial surveys (Forney et al. 1995), which covered a region overlapping the earlier MMS surveys and were similarly designed to survey all species of cetaceans. To the degree possible, we have reduced methodological biases and incorporated estimates of variance in the cetacean density and abundance estimates. Abundance estimates were stratified by season and year to examine seasonal and interannual variability in the study area. Estimated average abundance for the 1980-83 period also was compared statistically to estimates derived from the 1991-92 survey data to examine differences between the two periods.

Methods

MMS high-altitude aerial surveys

A description of the field and analytical procedures used for the MMS 1980-83 aerial surveys is provided in Dohl et al. (1983). Pertinent aspects of the methods, including information gathered during the reprocessing tasks, are summarized here.

Aerial line transect surveys were conducted monthly from March 1980 to February 1983. Each month, a subset of approximately 40 of the 92 pre-determined transects between Point Conception and the California-Oregon border (Figure 2.1) was surveyed. The monthly transects were selected a priori in an attempt to provide

uniform coverage of the study area on a seasonal basis. The study area transects were oriented east-west and spaced 5 nmi (9 km) apart; distances between the transects selected for each month was variable but usually larger. They were designed to survey systematically between the coast and approximately 90 nmi (167 km) offshore; however, the average distance offshore that was actually surveyed during the 3-year period was only about 75 nmi (139 km), presumably because of weather or logistic constraints. Each monthly survey spanned approximately 5 days, typically beginning in the south and proceeding north, and covered about 2,000 nmi. The nominal flight altitude was recorded as 1,000 ft (305 m) ASL (Dohl et al. 1983), although the database includes sightings recorded at altitudes of less than 500 ft (152 m) ASL and as high as 1,900 ft (579 m) ASL.

The survey platform was a high-wing, twin-engine Hunting Pembroke aircraft outfitted with a VLF-Omega onboard navigational computer. A radar altimeter was used to estimate aircraft height above the water. The survey team consisted of two observers (one on each side of the plane) and one data recorder who entered information onto sighting sheets in real-time. In addition to position, species sighted, and number of animals, the sighting sheets included entries for declination angle (in degrees) when abeam to the animals sighted, as well as flight altitude. The aircraft was diverted from the transect line in order to fly over animals for improved group size estimation and photography. Following species identification and enumeration, reciprocal courses were flown back to the transect line to resume the survey. Additional sightings recorded while the aircraft was diverted in this manner

were included in the original MMS sighting database and abundance analyses, creating a potential bias in sighting rates.

During the original data processing and analysis, Dohl et al. (1983) made a number of assumptions and analytical choices that limit data comparability to more recent studies, and they did not explicitly state some analytical details, which also prevents direct comparison with results of other studies. The available information suggests that the study area was divided into 5' x 5' grid cells bisected by the transect lines. Each grid cell was characterized by water depth, slope, and other “fixed” environmental characteristics that were entered into a digital file. Following each monthly survey, dynamic environmental data including Beaufort sea state conditions during the survey were entered into a separate file at the 5' x 5' grid cell resolution. Sighting data were recorded by latitude and longitude to the nearest 0.1', although the absolute accuracy of positions from VLF/Omega systems in aircraft often was uncertain by 0.5' to 1' (W.J. Richardson pers. comm. 2007). Positions were assigned to one of the 5' x 5' cells and eventually merged with the fixed and dynamic environmental files. Abundance analyses followed simple line-transect methods (Burnham et al. 1980) without consideration of covariates or stratification.

SWFSC California coast aerial surveys

Detailed descriptions of the SWFSC aerial survey field methods and analytical methods have been published previously (Carretta and Forney 1993;

Forney et al. 1995; Forney and Barlow 1998); pertinent aspects are summarized here.

SWFSC conducted aerial line-transect surveys off California in March-April 1991 and February-April 1992. The transects followed an overlapping grid (Figure 2.2) designed to survey systematically along the entire California coast out to 100 nmi off central and northern California and out to 150 nmi off southern California. The transect lines were spaced approximately 22-25 nmi apart.

The survey platform was a twin-engine, turbo-prop Twin Otter aircraft outfitted with two bubble windows for lateral viewing and a belly port for downward viewing. The plane was equipped with a radar altimeter to estimate height above the water. The survey team consisted of three observers: two “primary” observers who searched through the left and right bubble windows and a “secondary” observer who used the belly window to search the trackline and report sightings missed by the primary team. Using a primary and secondary observation team allowed for the estimation of the fraction of animals missed on the transect line. The survey team also included a data recorder who entered sighting information and updated environmental conditions throughout the survey using a laptop computer connected to the aircraft’s LORAN or GPS navigation system. The two primary observers used hand-held clinometers to measure declination in degrees to the animals sighted when abeam of the aircraft. The belly observer estimated angles based on tick marks applied to one edge of the window. Following line-transect methods, perpendicular distances were calculated based on the declination angle and the aircraft’s altitude.

Surveys were flown at 185 km/hr (100 knots) airspeed and 700 ft ASL altitude. When cetaceans were sighted, the aircraft circled over the animals to identify species and make group size estimates; any time the aircraft was diverted from the transect was considered “off effort” and additional cetacean sightings made during this time were not included in the abundance estimates.

Abundances were estimated using line-transect methods (Buckland et al. 2001) and as described in Forney et al. (1995) and Forney and Barlow (1998). For density estimation purposes, Forney et al. (1995) and Forney and Barlow (1998) used Akaike’s Information Criterion (AIC, Akaike 1973) to select among potential stratification variables, including area, group size category, species group, and Beaufort sea state. (AIC is an objective statistical measure used to obtain the best fit with the fewest parameters, attempting to optimize the trade-off between variance and bias in model predictions. It is calculated as $-2 \cdot \log\text{-likelihood} + 2 \cdot \text{number of parameters}$. Smaller values of AIC indicate a better model.) Variances in density estimates were estimated by a bootstrap method using samples consisting of 50 km segments of actual survey data that were randomly drawn with replacement to simulate 1,000 equivalent surveys. Abundances for all species were then recalculated from the bootstrap survey data and variances and coefficients of variation (CV) were obtained from the 1,000 new abundance values. The original abundance estimates derived from these data included corrections for perception bias and, for two species (Dall’s porpoise and sperm whale), approximate corrections for availability bias (Forney and Barlow 1998). Correction factors for perception and

availability bias were not included in the 1991-92 abundance estimates used for this study in order to facilitate a more consistent comparison to the 1980-83 data, for which such factors were not available.

Reprocessing the MMS high-altitude aerial survey data

In 2001, the MMS released the Marine Mammal and Seabird Computer Database Analysis System (CDAS; Bonnell and Ford 2001), a compact disc containing ship and aerial survey records off California, Oregon, and Washington from 1975 to 1997, including sighting and effort data from the 1980-83 high-altitude MMS surveys. The database contains separate files for sightings and survey effort with a field common to both files that identifies the effort date. In the case of the 1980-83 MMS surveys, the finest resolution available for effort dates is the midpoint of the two- to six-day period during which the survey occurred, creating a mismatch to sightings, which are identified by the actual date of the observation. For example, if the survey was flown on 10-14 March, the effort date for the entire survey is identified as 12 March. This is most likely an artifact of the way in which the original data were recorded: the effort database was created post hoc by interpolation from flight waypoints, sighting positions, and any other environmental observations recorded by latitude/longitude (Briggs, K.T. pers. comm. 2003). Thus, information such as sea state and flight altitude was available only for the sightings themselves, not for each unit of effort.

Line-transect methodology is considered “pooling robust” (i.e., data can be pooled over many factors that affect detection probability and still yield a reliable density estimate; Buckland et al. 2001). When heterogeneity in the data creates a notable difference in detection properties, however, bias can be reduced and precision increased by conducting a stratified analysis, i.e., estimating density separately for different environmental conditions, group sizes, altitudes, or geographic regions, and subsequently combining estimates to calculate total abundance (Buckland et al. 2001). The lack of information on sea state, altitude, and other factors associated with survey effort created the biggest challenge in reprocessing the MMS dataset using stratified methods that are consistent with those used in more recent studies. Following is a step-by-step description of the procedures used to reprocess the MMS survey data, including brief descriptions of the potential sources of bias and the methods we used to account for them. Major steps in the data analysis process and a comparison of 1980-83 and current methodologies are depicted in Figures 2.3a and 2.3b.

Oversampling. The CDAS effort file for the 1980-83 MMS survey is configured according to the original grid cells designated by Dohl et al. (1983), so that for every 5' x 5' grid cell, there is an associated mid-latitude and mid-longitude point. We merged the sighting file with the effort file by appending each sighting record to the effort segment whose mid-latitude and mid-longitude point was closest to the observation, thus creating a single database in flat file format. In addition to positional information, the effort file includes an approximate effort date as

described above and a field for the total distance (in km) flown in a single survey period within each grid cell. The latter varies from < 1 km to > 20 km, with the average distance reflecting the theoretical straight-line expectation for a given 5' segment of latitude. While some of the longer east-west segments are clearly due to additional flying required in "corner" segments, i.e., when moving off an east-west trending transect to head north or south to the next trackline (refer to Figure 2.1), there are many mid-transect segments that are much longer than the theoretical straight-line distance. These longer mid-transect segments may reflect situations where the survey team flew off the transect line to circle a group of animals in an attempt to improve group size estimates or to take pictures. Under standard line-transect methods (Buckland et al. 2001), this time should be considered "off effort" so that the distance flown, as well as any additional sightings that occur while off effort, are not included in the density calculations. We therefore adjusted all transect segments to equal no more than the theoretical straight-line 5' distance for the given latitude. Segments shorter than the theoretical straight-line expectation were not changed. Sightings on all of the longer segments were inspected and deleted if their recorded locations were well north or south of the primary east-west trending tracklines, indicating that they were most likely recorded while the aircraft was off effort. This resulted in deletion of approximately 4.46% of the sightings made from the primary transect lines. If some of these were actually on-effort sightings, our estimates may be biased downward. An additional seven sightings were deleted

because their recorded sighting locations were outside of the study area; six were in Oregon and a single sighting was recorded from the Southern California Bight.

Overlapping effort. For every month, sightings were plotted on maps of actual survey effort using ArcGIS (version 9.0, ESRI, Inc.), and the sighting attribute table was queried to provide information on date, sea state, and altitude of the survey effort. For example, for months with sufficient sightings, plots of sightings by date helped in the determination of effort date; if adjacent transects contained sightings separated by a day, it was clear where one survey day ended and the next began. Such determinations were only possible for those months containing many sightings. During 12 of the 36 survey months, sightings from different survey days were located along the same transect line, indicating that the transect line was flown more than once during the month, although the distance flown as shown in the effort file reflected only one pass. To prevent an upward bias in encounter rates, when sightings from two different survey days were located on the same transect line, one of the days was eliminated using the following criteria, in order of application: 1) altitude (days with sightings that deviated most from the target altitude of 1,000 ft); 2) sea state (days with sightings recorded at higher sea state values); and 3) random selection. This resulted in deletion of approximately 1.8% of the sightings made from the primary east-west trending tracklines. There could have been additional transect lines that were flown more than once per month with sightings recorded on only one (or neither) of the days, but it was impossible to make this determination from the available data.

Low altitude sightings. The sighting data indicate that survey flight altitudes ranged from 100 to 1,900 ft ASL. The majority of the sightings (86.06 percent) were recorded at the planned survey altitude of 1,000 ft ASL; only 2 percent of the sightings had recorded altitudes above 1,000 ft ASL and 4.6% had recorded altitudes below 500 ft ASL. Detection properties for surveys conducted at varying altitudes are expected to differ, because the visible swath beneath the aircraft narrows as flight altitude decreases. Ideally, these differences would be taken into account during the estimation of detection functions, either through stratification or using altitude as a covariate, but sample sizes were insufficient to do so.

Although altitude data for effort were not available, we conducted Kolmogorov-Smirnov (K-S) goodness-of-fit (GOF) tests of detection functions to assess differences between survey altitudes. Sightings with recorded altitudes that differed from the 1,000 foot standard were grouped into 5 altitude range categories to enable a comparative analysis (100-250, 300-475, 500-750, 800-994, and 1,040-1,900 ft ASL). Similar species were grouped to increase sample sizes in each altitude range, and the distributions of perpendicular sighting distances were compared to those obtained at the standard survey altitude of 1,000 ft. The species groups included medium-large whales, comprising sperm whale, gray whale (*Eschrichtius robustus*), humpback whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), and blue whale (*Balaenoptera musculus*); delphinids which included northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), and Risso's dolphin (*Grampus griseus*); and

porpoises, which included harbor porpoise (*Phocoena phocoena*) and Dall's porpoise. The K-S test results suggested that the distributions were not significantly different ($\alpha = 0.05$) for any of the species groups; however, statistical power to detect differences was low for altitudes below 500 ft ASL because sample sizes were small (< 10). For this reason, effort and associated sightings were deleted when sightings indicated that entire transects were flown at altitudes below 500 ft. This resulted in the deletion of approximately 1% of the sightings and $< 1\%$ of effort made from the primary east-west trending transect lines.

Cross legs. Sighting rates have been shown to vary with glare conditions (Forney et al. 1991), which are often a function of the aircraft heading. The MMS surveys were designed as a series of 92 parallel transect lines located perpendicular to the coast, requiring the aircraft to transit north or south between the primary transect lines. Both the effort and sightings associated with these cross legs were included in the original density estimates published by Dohl et al. (1983). We deleted these cross legs from our analysis, because 1) glare and detection properties are expected to be different on north-south vs. east-west transect lines, and 2) traveling parallel to the coast, particularly in the case of the nearshore cross legs, leads to oversampling portions of the study area. Furthermore, only one side of the aircraft was searched as they transited nearshore to the next transect line. Deleting the nearshore cross legs removed 349 sightings (16%) from the database; 70% of these were gray whale sightings. The deletion of offshore cross legs removed 95 sightings ($< 5\%$) from the database.

Missing sea state information. The detectability of cetaceans, particularly small, cryptic species, is affected by sea state conditions at the time of the survey (Barlow 1995). If sample size permits, estimation is often more precise and accurate when detection functions are estimated separately for sightings in calm waters without whitecaps (i.e., Beaufort 0-2 conditions) and in the presence of whitecaps (i.e., Beaufort 3-4;), or if density calculations are restricted only to calm conditions (Forney et al. 1991; Barlow 1995; Forney 1995; Carretta et al. 2001). This is particularly true for small or cryptic cetaceans. Objective statistical criteria, such as AIC, are generally used to determine the need for such stratification. This approach requires that effort data be designated by sea state.

For the MMS dataset, various methods were explored to deal with the missing sea state information including data exclusion, estimating sea state from archived sources of wind information such as historic buoy data or surface pressure maps, linear interpolation between sightings with known sea state values, weighted interpolation using time as a weighting factor, and more sophisticated interpolation procedures such as kriging. All of these approaches to estimating sea state were subject to much uncertainty. The method selected for this analysis involved a multi-step process that assigned sea state categories to effort based on available information from the sighting records. First, all sightings and transects flown per month were plotted using ArcGIS, and the sightings coded by sea state. All sightings recorded as Beaufort 5-6 and their associated transect lines were deleted. This resulted in the elimination of 8 primary transects (i.e., east-west trending)

totaling 713 km of effort and a total of 4 cetacean sightings ($< 1\%$ of the total sightings). All remaining transect lines were assumed to have been flown in Beaufort 0-4 conditions as suggested by the original investigators (M. Bonnell, pers. comm. 1997). Where sightings were sufficiently frequent, the underlying effort segments were designated as either Beaufort 0-2 or Beaufort 3-4 based on recorded sea states. Where sightings were sparse or sea state values were highly variable, effort was designated as 0-4.

Based on the reprocessed survey data, a total of 109,440 km were flown in sea state category of Beaufort 0 through 4. Sixteen of the 1,533 sightings had no corresponding sea state information. Of the remaining 1,517 sightings, more than 85% were recorded in Beaufort sea states of 0-2. Given the small number of sightings in Beaufort sea state conditions > 2 , reliable statistical tests for detection function differences in sea state category 3-4 could not be made for any of the species/species groups. For this reason, all sea states were pooled for analysis.

Density and abundance estimation

For the purpose of reducing bias in the density and abundance estimates caused by uneven geographic coverage, the study area was separated into four regions based on oceanographic boundaries and survey coverage. An attempt was made to equalize effort within each stratum to the degree possible in order to prevent potential bias resulting from over- or under-sampling subregions within each stratum. Off the California coast, major upwelling centers include Cape Mendocino,

Point Arena, Point Reyes, Point Sur, and Point Conception (Hickey 1979; Longhurst 2007). Three north-south strata were defined inshore of the 2,000-m isobath, with divisions at Cape Mendocino and Point Sur, and a fourth stratum covered the entire study area offshore of the 2,000-m isobath (Figure 2.4). Cape Mendocino was chosen as a dividing line between the “northern” and “north central” strata because the Mendocino Escarpment is recognized as a natural biogeographical boundary, with distinct oceanographic processes occurring north of the cape (Longhurst 2007). Point Sur was selected as the boundary between the north central and “south central” strata because Dohl et al. (1983) noted that south of Point Sur, winds were favorable for upwelling throughout most of the 3-year study period. For simplicity, the combined northern, north central, and south central strata will be referred to as the “inshore” stratum, because they cover the regions inshore of the 2,000-m isobath. The area of each region was calculated using ArcGIS; the total study area was defined to include the region between shore and the furthest offshore extent of the transect lines surveyed during the 3-year period (125,138 km²; Figure 2.4). Overall survey effort varied among strata, particularly between the offshore and inshore strata (Table 2.1).

The abundance of some species of cetaceans varies seasonally within the study area (Forney and Barlow 1998). To examine seasonal variability during 1980-83, density and abundance estimates were stratified into four 3-month seasonal periods. Oceanographic seasons vary annually in both timing and duration, with warming or cooling trends localized along different areas of the California coast and

of variable strength based on the extent of upwelling (Lynn and Simpson 1987; McGowan et al. 1998; Roemmich 1992; Collins et al. 2002). Long-term (1967-1991) monthly upwelling indices from three locations along the California coast show consistent highs in June and July and consistent lows in December and January (Pacific Fisheries Environmental Laboratory [PFEL] Coastal Upwelling Indices website¹). Further, the nearshore surface countercurrent generally develops and flows poleward along the California coast from November to January (Pares-Sierra and O'Brien 1989). Therefore, we adopted the following seasonal definition for this analysis: spring = February–April, summer = May–July, fall = August–October and winter = November–January. These seasons differ from those defined by Dohl et al. (1983) in the original analysis, but are consistent with more recent spring (Forney et al. 1995) and fall (Barlow 1995) surveys.

Dohl et al. (1983) do not describe how sighting declination angles were determined during the aerial surveys. The majority of the sighting declination angles recorded in the original database were rounded to the nearest five degrees (e.g., 5, 10, 15, etc.). In order to reduce the potential for clumped perpendicular distance distributions resulting from rounding errors, we smeared the declination angles by adding or subtracting random integer values from 0 to 2 prior to converting the angles to perpendicular distances.

Distributions of perpendicular sighting distances are often pooled across species when doing line-transect calculations in order to increase sample size and

¹ <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling>

reduce variance (Buckland et al. 2001). Following the methods of Barlow (1995) and Forney et al. (1995), we created preliminary species groupings and group size categories by combining perpendicular distance sighting distributions for species that were similar or occurred in mixed groups. The best stratification scheme was determined using an iterative approach of testing for significant differences between various species groupings and group size categories using a Kolmogorov-Smirnov test. Unidentified species were not included in the estimates, resulting in underestimation of true densities. The iterative testing approach resulted in 7 species group categories (Table 2.2).

Density and abundance for each season and species were estimated for all years pooled according to the standard line-transect formula (Buckland et al. 2001):

$$N_{h,k} = \sum_{i=1}^4 \sum_{j=1}^7 \frac{A_i n_{h,i,j,k} s_{h,i,j,k} f_j(0)}{2 L_{h,i}} \quad (\text{Eq. 2.1})$$

where

- $N_{h,k}$ = estimated total number of animals of species k in the study area during season h ;
- $n_{h,i,j,k}$ = number of sightings of groups of species k in group category j , during season h in geographic stratum i ;
- $s_{h,i,j,k}$ = mean group size for groups of species k in group category j , during season h in geographic stratum i , calculated as the total

number of animals in all groups divided by the number of groups sighted;

$f_j(0)$ = the probability density function evaluated at zero perpendicular distance, i.e., on the trackline, for group category j of the species group to which species k belongs (in km^{-1});

A_i = size of geographic stratum i (in km^2);

$L_{h,i}$ = length of transect line (in km) surveyed in geographic stratum i during season h .

An alternate formula that did not include geographic stratification was used to estimate seasonal abundances for the inshore stratum by year, y , because sample sizes were insufficient to stratify simultaneously by year, season, and geographic stratum:

$$N_{y,h,k} = \sum_{j=1}^7 \frac{A n_{y,h,j,k} s_{y,h,j,k} f_j(0)}{2 L_{h,i}} \quad (\text{Eq. 2.2})$$

where

$N_{y,h,k}$ = estimated total number of animals of species k in the study area during season h in year y ;

$n_{y,h,j,k}$ = number of sightings of groups of species k , in group category j , during season h in year y ;

- $s_{y,h,j,k}$ = mean group size for groups of species k , in group category j , during season h in year y ;
- $f_j(0)$ = the probability density function evaluated at zero perpendicular distance, i.e., on the trackline, for group category j of the species group to which species k belongs (in km^{-1});
- A = size of inshore stratum (in km^2);
- $L_{h,y}$ = length of transect line (in km) surveyed in year y during season h .

These yearly estimates were made only for the inshore stratum because the offshore stratum was not sampled proportionately; it represented 54% of the study area but included only 20% of the overall survey effort in the original analysis (Table 2.1). Following deletion of the areas furthest offshore that were never surveyed (Figure 2.4), the offshore stratum represented 49% of the study area and included 20% of the overall survey effort (Table 2.1). This uneven coverage would have resulted in biased estimates. Effort was more representative within the three sub-regions of the inshore stratum: for this study, the south-central stratum had 24% of the effort and 15% of the area; the north-central stratum had 37% of the effort and 23% of the area, and the northern stratum had 19% of the effort and 13% of the area.

Values for $f(0)$ were estimated for each species group by fitting the distribution of perpendicular sighting distances for all years and all regions combined to uniform, half-normal, and hazard-rate models using the program

DISTANCE (Thomas et al. 2002). Based on visual inspection of perpendicular sighting distributions at various scales, a left truncation distance of 162 m (531 ft) was selected to eliminate the blind spot beneath the aircraft. Right truncation distances for each species/species group were selected to eliminate the most distant 5% to 10% of the sightings (Buckland et al. 2001). The most parsimonious model was selected based on maximizing the chi-square goodness-of-fit statistic and minimizing AIC (Buckland et al. 2001).

Perpendicular distances were not recorded for 121 (7.9 percent) of the “on-effort” sightings in the final database. In order to account for these sightings in the density estimates, we randomly prorated them based on the perpendicular distance distributions for each species/species group. We therefore used mean group size for estimating density and abundance rather than a regression-based estimate (see below) because the latter is dependent on having perpendicular distance data for all sightings.

The probability of detection is often a function of group size, i.e., larger groups are easier to detect and are thus over-represented in the sample. Methods of reducing this potential size bias include stratifying by group size, or using regression-based estimates of mean group size. Buckland et al. (2001) recommend regressing the log of the observed group size against the estimated probability of detection at distance x . If the regression is significant at $\alpha = 0.15$, the regression-based estimate of mean group size at zero distance or the left-truncation distance (where, theoretically detection probability is maximal) is used in place of the mean

group size. In this study, potential group size bias was reduced by estimating densities separately for small groups and sightings of single species (vs. multiple species sightings). In addition, we ran regressions on each of the 7 species/species group categories using only the sightings for which perpendicular sighting distances were known. We found that evidence of group size bias remained for two categories: single species sightings of northern right whale dolphin, and multiple species sightings of Risso's, Pacific white-sided, and northern right whale dolphins. For these two species/species groups, we therefore used the average group size for the subset of sightings within a narrower strip width, for which there was no indication of size bias. In both cases this occurred where the probability of detection = 0.6, consistent with recommendations of Buckland et al. (2001).

In line-transect theory, $g(0)$ is the probability of detecting an animal or group of animals on the transect line. This probability is known to be less than 1 for aerial surveys of most cetaceans. Insufficient data are available to estimate the true probability of detection, and therefore the estimates reported here are minimum estimates because we assumed that $g(0) = 1.0$. The extent of underestimation will vary by species, depending on conspicuousness and on diving and schooling behavior.

Variance estimation

Precision of the density estimates was estimated analytically using the formula for stratified estimates (Buckland et al. 2001):

$$\text{var}(D) = D^2 \left(\frac{\text{var}(M)}{M^2} + \frac{\text{var}[f(0)]}{[f(0)]^2} \right) \quad (\text{Eq. 2.3})$$

where

$$M = \frac{\sum_v A_v M_v}{A}, \quad (\text{Eq. 2.4})$$

A_v = size of stratum area (in km^2)

$M_v = n_v s_v / l_v$ for stratum v , where $v = i$ (geographic stratum) or y (year),
and

$$\text{var}(M) = \frac{\sum_v A_v^2 \text{var}(M_v)}{A^2} \quad (\text{Eq. 2.5})$$

with

$$\text{var}(M_v) = M_v^2 \left(\frac{\text{var}(n_v)}{n_v^2} + \frac{\text{var}(s_v)}{s_v^2} \right) \quad (\text{Eq. 2.6})$$

Seasonal bootstrap comparison

Differences in seasonal abundance within the 1980-83 study period were examined using the confidence-interval-based procedure presented by Forney and Barlow (1998), and modeled after Lo's (1994) difference of means approach. Pairwise comparisons were made iteratively between the two seasons with the greatest difference in estimated abundance (excluding zeros). Only if the initial comparison was significant were further pair-wise comparisons made. For each

season, 1,000 abundance estimates, N^* , were generated by applying random lognormal deviates to the original point estimate of abundance and standard error (SE), in a manner similar to a parametric bootstrap (Efron and Tibshirani 1998). We used lognormal deviates since products (i.e., abundance estimates) theoretically have lognormal error distributions. In this case, we were not attempting to estimate the true population means, but rather testing the probability that the two samples came from the same distribution. Given the pair of 1,000 seasonal abundance estimates, $N^*_{\text{season 1}}$ and $N^*_{\text{season 2}}$, respectively, 1,000 difference values were calculated as $N^*_{\text{season 1}} - N^*_{\text{season 2}}$. A 95% confidence interval for each species was then calculated from this set of 1,000 difference values using the bias-corrected and accelerated (BC_a) method recommended by Efron and Tibshirani (1998). (The BC_a method provides a more accurate comparison than uncorrected percentile methods, because the latter assume the SE is constant rather than a function of sample size; BC_a corrects for this “acceleration” by accounting for how fast the SE changes with sample size.) Seasonal abundance estimates were determined to be significantly different at $\alpha = 0.05$ if the 95% confidence interval of their difference did not contain zero. This method has been shown to be robust to a variety of underlying error distributions, including the lognormal (Lo 1994). When significant seasonal differences were identified, testing continued using the two seasons with the second-largest difference in the point estimates. Testing continued in this way until the seasonal abundance difference was not identified as significant at $\alpha = 0.05$ or until all seasons had been tested.

Bootstrap comparison to 1991-92 estimates

For this comparison, cetacean abundances were re-estimated from the SWFSC 1991-92 aerial survey data for the smaller MMS study area using previously described methods (Forney et al. 1995; Forney and Barlow 1998). Corrections for perception and availability bias, i.e., $g(0)$, were not applied to these 1991-92 abundance estimates in order to maintain consistency with the 1980-83 estimates, for which estimates of $g(0)$ were not available. To statistically compare the new 1980-83 abundance estimates with those generated from the 1991-92 data for the same geographic region, we used the same confidence-interval-based procedure as described above for the seasonal comparison. In this case we computed differences in 1,000 bootstrap abundance estimates for the 1980-83 and 1991-92 periods. For the 1980-83 data, 1,000 abundance estimates were generated by applying random lognormal deviates to the original point estimate of abundance and SE as described above. For the 1991-92 data, 1,000 bootstrap abundance estimates, N^* , were produced following the methodology described in Forney and Barlow (1998) but using the smaller MMS study area.

Results

1980-83 seasonal abundance estimation

A total of 2,124 cetacean sightings of 16 species and two genera (which could not be identified to species) were made during the 36 monthly MMS high-altitude surveys. Following reprocessing, a total of 1,533 sightings (72.2% of the

original total) remained in the final database used for density and abundance estimation (Table 2.3). Density estimates were not made for whales belonging to the genus *Kogia*, short-finned pilot whale (*Globicephala macrorhynchus*), sei whale (*Balaenoptera borealis*), minke whale (*Balaenoptera acutorostrata*), Cuvier's beaked whale (*Ziphius cavirostris*), Baird's beaked whale (*Berardius bairdii*), and beaked whales belonging to the genus *Mesoplodon*, due to the limited numbers of sightings available for estimation of their detection functions. In addition, density estimates were not made for the gray whale or harbor porpoise because the broad MMS survey design was not appropriate for either of these species. They occur within a narrow coastal band and are generally assessed using focused (single-species) nearshore surveys (Forney et al. 1991; Buckland et al. 1993; Carretta et al. 2001). Of the remaining nine species, five species were represented by 118-250 sightings each, and four species were represented by 16-31 sightings each. The latter four species (and one of those with > 100 sightings) were medium-large whales, and were treated together for purposes of estimating the detection function. The number of sightings and average group size were seasonally variable for the majority of species for which we derived density and abundance estimates (Table 2.4).

The perpendicular distance data for all species/species groups were best modeled with a hazard-rate model and a left truncation distance of 162 m (531 ft) (Figure 2.5). The left truncation distance was identical to that used by Dohl et al. (1983). Separate models were selected based on AIC for single-species of small cetaceans, mixed-species groups of northern right whale dolphins, Pacific white-

sided dolphins, and Risso's dolphins, and for small groups (1-2 individuals) vs. large groups (3+ individuals) of Dall's porpoise (Table 2.2). All medium to large whales were combined.

Statistical comparisons cannot be made between the revised abundance estimates presented here and the original estimates reported by Dohl et al. (1983); however, point estimates provide a representative comparison (Table 2.5). All of the density and abundance estimates resulting from reprocessing and reanalyzing the 1980-83 high-altitude aerial survey data are lower than the estimates derived by the original researchers based on both the high- and low-altitude survey data (see Discussion).

Geographically stratified estimates were derived by pooling data across all 3 years, providing an indication of average seasonal distribution in the study area (Tables 2.6a and 2.6b). Annually stratified estimates provide a measure of interannual variability in seasonal patterns within the inshore portion of the study area (i.e., inshore of the 2,000-m isobath) during 1980-83 (Tables 2.7a and 2.7b). The geographically stratified abundance estimates appeared seasonally variable for all species considered (Table 2.6b). Within the nearshore stratum, seasonal differences between each of the years were evident for most species and were most pronounced for Pacific white-sided dolphin (Table 2.7b). The geographically stratified estimates are expected to be more accurate because they account for geographic heterogeneity. However, both sets of estimates are biased low because the probability of detecting an animal on the trackline, $g(0)$, was not taken into

account, i.e., was treated as if it were 1.0. In addition, unidentified animals were not included in the density estimates.

Statistically significant differences in seasonal abundance were evident for six of the nine species evaluated (Table 2.8). Bootstrap comparisons did not identify a significant difference in seasonal abundance for Risso's dolphin or northern right whale dolphin, despite the appearance of seasonal variability in the point estimates (Table 2.8). The abundances of both Dall's porpoise and Pacific white-sided dolphin in fall (August-October) were determined to be significantly different ($p = 0.003$ and $p = 0.004$, respectively) from those in spring (February-April). As expected given their seasonal migration patterns (Calambokidis et al. 2001, 2003), the abundances of blue and humpback whales were found to be significantly higher during the August-October time period compared to the other seasons.

Comparison to 1991-92 SWFSC abundance estimates

Only five species were sighted in sufficient numbers during both the 1980-83 and 1991-92 surveys to be included in the statistical comparison (Table 2.9). No significant differences in abundance were identified for Risso's dolphin, Pacific white-sided dolphin, northern right whale dolphin, or humpback whale. Dall's porpoise was more abundant during the 1991-92 surveys ($p = 0.04$).

Neither blue whales nor fin whales were sighted in spring during either survey in this portion of the study area. Killer whales (*Orcinus orca*) and sperm whales were sighted during spring in 1980-83 but were not recorded in this area

during the 1991-92 surveys. The lack of sightings in 1991-92 was to be expected given the low numbers seen in spring 1980-83 (Table 2.4) and the lesser survey coverage in 1991-92. Conversely, common dolphins (*Delphinus* spp.) and bottlenose dolphins (*Tursiops truncatus*) were both sighted in 1991-92 but were not sighted in the entire study area during the 1980-83 high-altitude MMS surveys; there were two sightings of common dolphins during the low-altitude surveys in this area (Dohl et al. 1983). It is surprising how few common dolphin sightings there were during 72 surveys covering the 3-year period, especially given the high numbers of sightings of this species during recent surveys (Barlow 1995; Forney et al. 1995; Barlow and Gerrodette 1996; Benson et al. 2002; Barlow 2003).

Discussion

Comparison to Dohl et al. (1983) estimates

The revised abundance estimates presented here are lower than the original estimates reported by Dohl et al. (1983). The actual $f(0)$ estimates used by Dohl et al. were not reported in their 1983 report; however, $f(0)$ estimates provided by M. Bonnell (pers. comm. 1997) for MMS high-altitude surveys off California were similar to those used here and probably did not contribute to the differences in density estimates. It is apparent that several other factors introduced substantial upward biases in the analysis presented by Dohl et al. (1983), including 1) the inclusion of sightings and effort on transit legs between transects, 2) the apparent inclusion of off-effort sightings and sightings from transects flown more than once in

the original analysis, without incorporation of the additional effort, 3) an inflated study area size (140,000 km²) that included offshore regions never surveyed, and 4) the lack of geographic stratification to account for the over-sampling of nearshore, high-density areas compared to offshore, low-density areas. Biased sampling is likely most responsible for Dohl et al.'s (1983) inflated density estimates, because density estimates derived primarily for shelf and slope waters, where animals are more abundant (Table 2.6a), were extrapolated to offshore regions where there was little or no survey effort (Table 2.1) and population densities are lower.

As noted by Dohl et al. (1983), group size bias also may have contributed to inflated density estimates, particularly for species with highly variable group sizes ranging from one to several thousand animals (e.g., Pacific white-sided dolphin, northern right whale dolphin). Another factor that may have contributed to the difference between the revised and original density estimates involves the way in which Dohl et al. combined data from both the high- and low-altitude surveys to derive overall mean density values. After densities were estimated by species and season for each 5' x 5' cell, larger 15' x 15' quadrats were established and density estimates from the smaller cells were averaged to yield new density values. The quadrat density estimates from the high- and low-altitude surveys were then averaged to provide relative densities and abundance estimates for the entire study area. The same methodology was used to estimate densities from the low-altitude surveys. Thus, all of the factors contributing to overestimation of the high-altitude density estimates also apply, resulting in exaggerated estimates derived from the

low-altitude surveys. The mean estimates from the combined surveys are thus derived from two sets of overestimated values.

For this study, reliance on sighting data collected from only the high altitude (1,000 foot ASL) MMS surveys likely resulted in an underestimation of abundance for small species that are difficult to see from the air such as Dall's porpoise. Survey effort was similar for the high- and low-altitude surveys, yet there were twice as many sightings of Dall's porpoise during the low altitude surveys, despite the limited lateral visibility at 200 feet ASL (Dohl et al. 1983). In addition, Dohl et al. (1983) noted that despite the higher number of sightings and larger mean group size of Risso's dolphins recorded from the high-altitude surveys, densities for this species were estimated to be higher when only low-altitude data were used. They attributed this difference to their estimate of $f(0)$, which was 4.6 times larger for the low-altitude data. For all species, estimates of $f(0)$ were up to six times larger for the low-altitude surveys and resulted in abundance estimates that were consistently higher than those estimated from the high-altitude data.

Dohl et al. (1983) only provided analytical confidence intervals for abundance estimates of a few species and their variance calculations did not include group size variance, which can significantly affect variance in density. Therefore, the 95% confidence intervals presented by Dohl et al. (1983) are likely too narrow and the CVs underestimated. In this study, CVs were calculated for all species according to recommendations in Buckland et al (2001) and included the stratified estimates of variance in mean group size. Both the point estimates and the variances

reported here are expected to be more accurate than those presented in Dohl et al. (1983).

Patterns of seasonal abundance, 1980-83

The revised 1980-83 abundance estimates reveal variability in both seasonal and interannual patterns for the species considered (Tables 2.6b and 2.7b). The abundance of Dall's porpoise and Pacific white-sided dolphin was determined to vary significantly ($p = 0.03$ and $p = 0.04$, respectively) with season. More animals were present in the study area during fall (August-October) than spring (February-April) (Table 2.6b). Both of these species had relatively lower variance estimates for the seasons compared (CVs ranging from 0.30-0.44; Table 2.6b) than did Risso's dolphin and northern right whale dolphin (CVs ranging from 0.40-1.16; Table 2.6b). For the latter two species, no significant difference in seasonal abundance was found, despite highly variable point estimates. Interannual variability was high for all of the small odontocetes considered (Table 2.7b), and results from this study support evidence presented by Forney and Barlow (1998) that interannual variability for these species can be as high as, or greater than, seasonal variability.

Statistically significant seasonal differences in abundance were evident for all of the medium-large whale species considered, except for sperm whale (Table 2.8). Seasonal differences in the abundance of blue and humpback whales were expected given their known foraging patterns off California during summer and fall; blue whales are present from roughly June through November and humpback whales May

through November (Calambokidis et al. 2001, 2003). Abundance estimates for both these species were highest during the August to October period, consistent with known distribution patterns. Seasonal abundance comparisons for fin whale were also consistent with known distribution patterns which indicate an increase in numbers of this species in summer and fall (Forney and Barlow 1998). The abundance of killer whales was also found to be significantly different among seasons, with more animals present during August through October than November through January. This result was surprising given the few sightings (3 in each season) and large variances (> 0.77) associated with the abundance estimates, and this result is inconsistent with past studies that indicate a lack of seasonal pattern for killer whales (Forney and Barlow 1998).

The annual estimates presented here (Table 2.7b) reflect interannual variability in seasonal abundance in the inshore portions of the study area during 1980-83. Part of the survey period overlapped a very strong El Niño-Southern Oscillation (ENSO) event, which is a disruption in the ocean-atmosphere system that results in the development of abnormally warm sea surface temperatures (SSTs) across the eastern tropical Pacific (Cane 1983; Fiedler 2002). During the 1982-83 ENSO event, many marine species exhibited considerable shifts in population distributions in the northeastern Pacific (Barber and Chavez 1983; Pearcy and Schoener 1987). These shifts included at least one cetacean species, the bottlenose dolphin (Wells et al. 1990). Because the majority of cetacean species are highly mobile, it is expected that an ENSO event would result in changes in local cetacean

abundance and distribution in response to the change in oceanographic conditions and availability of prey. Previous studies have documented large shifts in the distribution of Dall's porpoise in the study area, suggesting that these animals prefer regions of cooler, upwelling-modified water (Forney and Barlow 1998; Forney 2000). However, during the MMS surveys, the highest numbers of Dall's porpoise occurred during the time when water temperatures were elevated due to the ENSO event (i.e., August 1982-February 1983). It is possible that reduced upwelling during the 1982-83 El Niño concentrated Dall's porpoise in some of the surveyed regions as documented for humpback whales in Monterey Bay, CA, during the 1997-98 El Niño (Benson et al. 2002). Therefore, the apparent increase in Dall's porpoise density during ENSO could be an artifact of survey design.

Comparison to 1991-92 spring abundance estimates

The methodology used to derive the new density and abundance estimates for 1980-83 is comparable to that used for more recent aerial surveys, allowing evaluation of population changes during spring over the 10-year period (Table 2.9). The abundance estimates appear highly variable between 1980-83 and 1991-92; however, of the five species tested, a significant difference in abundance was identified for only one species, Dall's porpoise. This could be due in part to the high CVs (i.e., greater than 0.42) estimated for the other four species tested. Also, the power to detect significant differences was low, in part due to inadequate sample size; with the exception of Dall's porpoise, the 1991-92 surveys provided fewer than

six sightings per species. This compares to greater than 28 sightings available for all species except humpback whale from the February to April time frame of the 1980-83 surveys. The difference in sample size between the two survey periods highlights the value of the intensive survey coverage achieved in 1980-83 during each season.

The 1991-92 spring abundance estimate of Dall's porpoise in the inshore portion of the MMS study area (1,733 animals) was more than three times higher than during 1980-83 (574 animals), and this difference was determined to be significantly different ($p = 0.04$). The precision of the 1980-83 and 1991-92 estimates was similar (0.34 and 0.36, respectively). The $f(0)$ values used to estimate densities were also similar, as the $f(0)$ value of 4.70 used for the 1991-92 densities falls almost directly between the $f(0)$ values of 6.25 (for 1-2 animals) and 3.66 (for group sizes > 2) used to estimate densities for 1980-83. As noted above, use of the high altitude (1,000 feet ASL) 1980-83 survey data may have contributed to an underestimation of Dall's porpoise abundance in this study.

Biases and caveats

The present analysis successfully eliminated or reduced several key sources of bias that were present in the original analysis of 1980-83 MMS survey data (Dohl et al. 1983), but several sources of bias remain. The age of the data, coupled with technological limitations during the original data collection and processing, caused some information to be lost or insufficiently recorded and required a number of assumptions to be made. This was particularly true of the effort data, for which the

now-available information did not include sea state, survey altitude, or specific survey dates. Each of these could be approximated from information in the sightings file, but some of the details were missing. The examination of sea states associated with sightings by geographic region suggested that the majority of effort was conducted during near-calm conditions (Beaufort sea states of 0-2), and that the estimation would be robust to pooling of sightings made in varying sea states. In the absence of effort-specific sea state information, there is no way to evaluate this assumption, potentially introducing a downward bias of unknown magnitude.

Many sources of bias related to data collection from an aircraft, e.g., availability bias, are assumed to be similar for the 1980-83 and 1991-92 aerial surveys, allowing direct comparisons of relative abundance estimates. However, the different aircraft configurations used for the two surveys affected the field of view and therefore the detectability of cetaceans with respect to distance from the transect line. The reduced visibility resulting from the flat windows used during the 1980-83 surveys is partially taken into account in the detection function, $f(0)$, as the left truncation distance represents the approximate outer edge of the blind spot directly beneath the plane. Both studies assume a probability equal to 1 of detecting animals at zero perpendicular distance (e.g. below the aircraft for the 1991-92 data and at the truncation distance of 162 m for the 1980-83 data). It is likely, however, that the degree to which this assumption was violated varied between the two time periods. A separate experiment examining the probability of detection using these two different aircraft configurations would be required to assess potential differences.

We did not incorporate any correction factors for $g(0)$, the probability of detecting an animal or group of animals on the transect line, despite the fact that correction factors for perception bias were available for all species sighted in 1991-92. This probability is known to be less than 1 for aerial surveys of most cetaceans and therefore the estimates reported here are biased downward to a degree dependent on the species' diving and schooling behavior.

Conclusions

The density and abundance estimates reported in this study were derived using more advanced line transect analysis techniques than the original analysis of Dohl et al. (1983) and, therefore, provide a more accurate indication of cetacean abundance and distribution patterns off central and northern California during 1980-83. The re-analysis eliminated several sources of upwards bias present in the original analysis, resulting in revised density and abundance estimates that are much lower than the original estimates derived from the survey data. Although more accurate, the estimates reported here are biased downward from the true density because not all sources of bias could be accounted for. Estimates of precision were calculated analytically. Thus, they permit quantitative comparisons within the dataset and with abundance estimates derived from other aerial survey datasets analyzed using similar methodology.

Year-to-year (1980-83 vs. 1991-92) comparisons of spring (February-April) abundance inshore of the 2,000-m isobath showed a significant difference for only

one species, Dall's porpoise, despite the very different point abundance estimates for all five species considered. As for the seasonal comparisons, the abundance estimates for the remaining four species had high variances ($CVs > 0.40$) as compared to those of Dall's porpoise ($CVs < 0.40$). Based on the limited information from this study, it is impossible to determine if the significant difference in abundance between the early 1980s and early 1990s evident for Dall's porpoise is indicative of a long-term trend, interannual variability, or a result of differences in survey conditions. The limited numbers of sightings available from the 1991-92 surveys contribute to low statistical power; had the 1980-83 monthly survey effort been repeated a decade later, our power to detect any trend would have been far greater. Temporal and spatial variability in species distribution and abundance often result in a low statistical power to detect trends (Gerrodette 1987; Forney et al. 1991; Edwards and Perkins 1992; Forney 1999). Cetaceans often respond to oceanographic variability by moving over large geographical distances to locate suitable habitats, and regions such as California that exhibit high environmental variability present an even greater challenge in tracking population trends (Forney 2000). Both the 1980-83 and the 1991-92 survey periods were characterized by cool water conditions (1980 and 1991) that shifted to anomalously warm water conditions (1982-83 and 1992), particularly in the case of the 1982-83 ENSO event. It is not known how similar or different conditions were in localized areas of the study region and how these conditions might have affected the distribution of cetacean species during these periods. Further studies of the oceanographic conditions in the study

area at the times of the surveys are needed to improve our understanding of these findings.

Our ability to identify seasonal distribution patterns and detect trends in population would be greatly enhanced with the completion of additional comprehensive surveys like those of 1980-83, particularly given recent analytical developments in line-transect methodology (e.g., the inclusion of covariates in detection functions) and cetacean-habitat modeling (i.e., spatial modeling using environmental predictor variables). This study re-assessed the valuable data collected during the 1980-83 high-altitude surveys; however, this effort would have been enhanced if all of the original effort and environmental data had been archived for retrospective analyses such as these. Researchers involved with the major 1980-83 survey programs were aware of the importance of comprehensive effort and environmental data, e.g., sea state, and recorded this information in some form at the time of the surveys. The computer database that was created for MMS almost twenty years after the surveys were completed is a valuable source of information and enabled our re-analysis. However, some of the original data were lost in the interim. This highlights the importance of thorough data archival processes and creation of detailed metadata, so that data collected during current research efforts can be reassessed as technological and analytical methods improve.

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Table 2.1. Comparison of MMS survey effort (km) and area (km²) for the geographic strata used to estimate cetacean density and abundance in this study as compared to those listed by Dohl et al. (1983).

<i>This study:</i>	Total	Northern	North Central	South Central	Offshore
Effort (km)	109,440	21,124 (19%)	40,485 (37%)	26,513 (24%)	21,318 (20%)
Area (km²)	125,138	16,904 (13%)	28,573 (23%)	18,672 (15%)	60,989 (49%)
<i>Dohl et al. 1983:</i>					
Effort (km)	136,298	25,426 (19%)	50,247 (37%)	33,185 (24%)	27,440 (20%)
Area (km²)	140,000	16,904 (12%)	28,573 (21%)	18,672 (13%)	75,851 (54%)

Table 2.2. Species groups used for estimation of detection functions. The detection function accounts for the reduced probability of detecting a group of animals as their distance from the transect line increases. The number of groups sighted (n) is the total following application of both left (162 m) and right (species specific) truncation distances (RTD) and includes only those sightings for which perpendicular distances were recorded. Effective strip width (ESW) = $1/f(0)$.

Species ¹	Group Category	n	f(0)	CV (f(0))	RTD (km)
Dall's porpoise	group size 1-2	71	6.25	0.26	2.00
	group size > 2	84	3.66	0.15	2.00
Risso's dolphin (Gg)	single species sightings	165	2.06	0.13	1.95
Pacific white-sided dolphin (Lo)	single species sightings	82	2.40	0.16	1.50
Northern right whale dolphin (Lb)	single species sightings	32	3.67	0.58	2.00
Multiple: Gg, Lo, Lb	multiple species sightings	60	1.30	0.11	3.00
Killer whale	medium-large whale ²	10	1.85	0.27	2.50
Sperm whale	medium-large whale	26	1.85	0.27	2.50
Blue whale	medium-large whale	9	1.85	0.27	2.50
Fin whale	medium-large whale	16	1.85	0.27	2.50
Humpback whale	medium-large whale	66	1.85	0.27	2.50

¹ In addition to the above, there were 54 sightings of unidentified cetaceans that were not included in the analyses.

² The medium-large whales were analyzed as one group.

Table 2.3. Number of groups sighted (n) and mean group size (gs) for all identified cetacean species in the reprocessed database. Note that some of the “n” values are higher than listed in Table 2.2 because there were sightings for which perpendicular distances were missing; these could not be used to estimate detection functions but were used to estimate densities.

Species ¹	n	gs
Dall's porpoise, <i>Phocoenoides dalli</i>	204	4.15
Harbor porpoise, <i>Phocoena phocoena</i>	134 [†]	1.96
Risso's dolphin, <i>Grampus griseus</i>	250	62.90
Pacific white-sided dolphin, <i>Lagenorhynchus obliquidens</i>	156	170.35
Northern right whale dolphin, <i>Lissodelphis borealis</i>	118	216.66
Short-finned pilot whale, <i>Globicephala macrorhynchus</i>	3*	11.33
Unid. pygmy/dwarf sperm whale, <i>Kogia</i> , spp.	1*	3.00
Baird's beaked whale, <i>Berardius bairdii</i>	11*	4.45
Cuvier's beaked whale, <i>Ziphius cavirostris</i>	3*	1.33
Mesoplodon beaked whales, <i>Mesoplodon</i> spp.	1*	1.00
Killer whale, <i>Orcinus orca</i>	16	6.31
Sperm whale, <i>Physeter macrocephalus</i>	31	3.00
Blue whale, <i>Balaenoptera musculus</i>	21	1.43
Fin whale, <i>Balaenoptera physalus</i>	20	1.75
Sei whale, <i>Balaenoptera borealis</i>	1*	2.00
Humpback whale, <i>Megaptera novaeangliae</i>	124	3.04
Gray whale, <i>Eschrichtius robustus</i>	383 [†]	2.44
Minke whale, <i>Balaenoptera acutorostrata</i>	2*	1.00
Total	1,479	NA

¹ In addition to the above, there were 54 sightings of unidentified cetaceans that were not included in the analyses.

* Excluded from analysis due to low sample size.

† Excluded from analysis due to nearshore distribution.

Table 2.4. Number of groups sighted (n) and mean group size (gs) by season for cetacean species for which density and abundance estimates were made. The number of groups sighted is the total following application of both left (162 m) and right (species-specific; see Table 2.2) truncation distances and includes all sightings used to estimate densities, i.e., those for which perpendicular distances were recorded as well as a proportion of sightings missing distance information (see Methods: Density and Abundance Estimation). For single species sightings of northern right whale dolphin and multiple species sightings of Risso's dolphin, Pacific white-sided dolphin, and northern right whale dolphin, average group size within a truncated perpendicular distance was used to eliminate size bias (see Methods: Density and Abundance Estimation).

Species	Group Category	Feb-April		May-July		Aug-Oct		Nov-Jan	
		n	gs	n	gs	n	gs	n	gs
Dall's porpoise	group size 1-2	10	1.60	14	1.71	31	1.61	21	1.90
	group size > 2	21	4.43	14	4.79	28	4.46	27	5.04
Risso's dolphin	single species	39	13.03	52	17.31	44	30.00	38	46.24
	multiple species	15	161.89	14	161.89	16	161.89	3	161.89
Pacific white-sided dolphin	single species	21	36.43	16	50.56	36	122.97	16	65.31
	multiple species	12	264.75	13	264.75	14	264.75	8	264.75
Northern right whale dolphin	single species	9	124.00	1	124.00	9	124.00	14	124.00
	multiple species	21	112.57	16	112.57	22	112.57	12	112.57
Killer whale	med-large whale	3	4.33	4	2.75	3	22.00	3	2.00
Sperm whale	med-large whale	7	2.43	0	NA	5	9.00	18	1.67
Blue whale	med-large whale	0	NA	0	NA	17	1.35	1	1.00
Fin whale	med-large whale	0	NA	1	6.00	13	1.69	4	1.00
Humpback whale	med-large whale	1	2.00	12	3.58	84	2.85	13	4.77

Table 2.5. Comparison of seasonal density (D; number of animals/km²) and abundance (N) point estimates for the present study and those presented in Dohl et al. (1983). Abundance estimates are for the entire study area; Dohl et al. assumed the study area = 140,000 km² while the present study assumed the study area = 125,138 km². The estimates for this study are based on a stratified analysis and are expected to be more accurate because several sources of bias were removed or minimized. Estimates are provided in the seasonal divisions used by Dohl et al. (1983): winter = December-February, spring = March-May, summer = June -August, and fall = September-November. Note that these seasons are different than those used in this study, so that the density and abundance estimates provided in subsequent tables are different than shown here.

Species ¹	Dec-Feb		Mar-May		June-Aug		Sept-Nov	
	D	N	D	N	D	N	D	N
Risso's dolphin								
This study	0.0706	8,832	0.0431	5,397	0.0809	10,124	0.0678	8,485
Dohl et al. 1983	0.2132	30,000	0.1066	15,000	0.0924	13,000	0.1422	20,000
Dall's porpoise								
This study	0.0071	885	0.0030	372	0.0086	1,080	0.0149	1,862
Dohl et al. 1983	0.0244	3,400	0.0256	3,600	0.0261	3,700	0.0622	8,750
Pacific white-sided dolphin								
This study	0.0745	9,319	0.0527	6,590	0.1610	20,142	0.2072	25,930
Dohl et al. 1983	0.2382	33,500	0.1869	26,000	0.2271	32,000	0.6120	86,000
Northern right whale dolphin								
This study	0.1286	16,094	0.0487	6,092	0.0862	10,785	0.2154	26,961
Dohl et al. 1983	0.44	61,500	0.21	29,000	0.19	27,000	0.27	37,500

¹Included are those species for which Dohl et al. provided seasonal density estimates.

Table 2.6a. Minimum density estimates (D) and coefficients of variation (CV), by geographic stratum, for the most common cetacean species sighted during the MMS 1980-83 aerial surveys. Estimates do not include correction factors for perception or availability biases, $g(0)$.

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	D	CV	D	CV	D	CV	D	CV
Risso's dolphin								
Northern	0.008	0.70	0.033	0.62	0.047	0.55	0.037	0.97
North central	0.053	0.46	0.125	0.30	0.084	0.38	0.040	0.44
South central	0.192	0.35	0.069	0.48	0.326	0.30	0.228	0.51
Offshore	0.007	0.59	0.081	4.49	0.011	0.95	0.012	0.70
Inshore Stratum	0.082	0.42	0.084	0.36	0.144	0.35	0.094	0.51
Total study area	0.045	0.40	0.083	0.90	0.079	0.33	0.054	0.47
Dall's porpoise								
Northern	0.005	0.49	0.002	0.72	0.009	0.42	0.019	0.33
North central	0.006	0.39	0.012	0.29	0.027	0.24	0.016	0.27
South central	0.017	0.30	0.003	0.60	0.009	0.37	0.012	0.43
Offshore	0.000	0.00	0.005	0.53	0.008	0.43	0.007	0.52
Inshore Stratum	0.009	0.34	0.007	0.38	0.017	0.32	0.016	0.31
Total study area	0.005	0.34	0.006	0.35	0.013	0.30	0.011	0.29
Pacific white-sided dolphin								
Northern	0.072	0.69	0.031	1.04	0.037	1.05	0.139	0.58
North central	0.120	0.50	0.185	0.40	0.379	0.45	0.055	0.58
South central	0.151	0.46	0.083	0.70	0.545	0.56	0.141	0.50
Offshore	0.035	0.90	0.095	6.26	0.139	0.51	0.089	0.82
Inshore Stratum	0.116	0.45	0.115	0.48	0.337	0.45	0.102	0.43
Total study area	0.077	0.44	0.105	0.98	0.241	0.39	0.096	0.45
Northern right whale dolphin								
Northern	0.105	0.99	0.013	1.02	0.031	0.75	0.029	0.74
North central	0.128	0.69	0.047	0.45	0.063	0.43	0.100	0.81
South central	0.211	0.68	0.084	0.71	0.256	0.71	0.259	0.95
Offshore	0.013	1.00	0.054	4.67	0.272	0.98	0.237	1.10
Inshore Stratum	0.146	0.71	0.049	0.50	0.111	0.57	0.128	0.86
Total study area	0.081	0.66	0.052	1.16	0.189	0.87	0.181	1.02

Table 2.6a (continued).

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	D	CV	D	CV	D	CV	D	CV
Killer whale								
Northern	0.000	0.00	0.000	0.00	0.000	0.00	0.001	0.90
North central	0.001	0.74	0.001	0.88	0.006	1.04	0.000	1.03
South central	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.00
Offshore	0.000	0.00	0.000	0.00	0.000	1.03	0.000	0.00
Inshore Stratum	0.001	0.87	0.000	0.95	0.003	1.04	0.000	0.77
Total study area	0.000	0.87	0.000	0.95	0.002	0.94	0.000	0.77
Sperm whale								
Northern	0.000	0.89	0.000	0.00	0.005	1.02	0.002	1.02
North central	0.000	0.90	0.000	0.00	0.000	1.02	0.001	0.47
South central	0.000	0.00	0.000	0.00	0.001	1.02	0.000	1.02
Offshore	0.002	0.88	0.000	0.00	0.002	1.00	0.002	0.52
Inshore Stratum	0.000	0.72	0.000	0.00	0.002	0.83	0.001	0.62
Total study area	0.001	0.87	0.000	0.00	0.002	0.70	0.001	0.54
Blue whale								
Northern	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.00
North central	0.000	0.00	0.000	0.00	0.001	0.51	0.000	1.02
South central	0.000	0.00	0.000	0.00	0.001	0.55	0.000	0.00
Offshore	0.000	0.00	0.000	0.00	0.001	0.80	0.000	0.00
Inshore Stratum	0.000	0.00	0.000	0.00	0.001	0.56	0.000	1.03
Total study area	0.000	0.00	0.000	0.00	0.001	0.52	0.000	1.03
Fin whale								
Northern	0.000	0.00	0.000	0.00	0.000	0.00	0.000	0.00
North central	0.000	0.00	0.000	0.00	0.000	0.96	0.000	0.63
South central	0.000	0.00	0.001	1.01	0.001	0.54	0.000	1.02
Offshore	0.000	0.00	0.000	0.00	0.001	0.50	0.000	0.00
Inshore Stratum	0.000	0.00	0.000	1.02	0.001	0.62	0.000	0.67
Total study area	0.000	0.00	0.000	1.02	0.001	0.55	0.000	0.67
Humpback whale								
Northern	0.000	0.00	0.000	1.03	0.001	1.03	0.000	0.00
North central	0.000	0.00	0.001	1.02	0.020	0.38	0.005	0.70
South central	0.000	1.02	0.004	0.62	0.004	0.51	0.000	1.02
Offshore	0.000	0.00	0.002	0.68	0.002	0.54	0.000	0.00
Inshore Stratum	0.000	1.03	0.001	0.67	0.010	0.53	0.002	0.81
Total study area	0.000	1.03	0.002	0.59	0.006	0.48	0.001	0.81

Table 2.6b. Minimum abundance estimates (N) and coefficients of variation (CV), by geographic stratum, for the most common cetacean species sighted during the MMS 1980-83 aerial surveys. Estimates do not include correction factors for perception or availability biases, $g(0)$.

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	N	CV	N	CV	N	CV	N	CV
Risso's dolphin								
Northern	131	0.70	552	0.62	792	0.55	628	0.97
North central	1,517	0.46	3,561	0.30	2,389	0.38	1,142	0.44
South central	3,590	0.35	1,294	0.48	6,078	0.30	4,258	0.51
Offshore	399	0.59	4,947	4.49	679	0.95	724	0.70
Inshore Stratum	5,237	0.42	5,406	0.36	9,258	0.35	6,028	0.51
Total study area	5,636	0.40	10,353	0.90	9,937	0.33	6,752	0.47
Dall's porpoise								
Northern	85	0.49	41	0.72	159	0.42	317	0.33
North central	174	0.39	357	0.29	758	0.24	469	0.27
South central	315	0.30	65	0.60	168	0.37	218	0.43
Offshore	0	0.00	308	0.53	484	0.43	398	0.52
Inshore Stratum	574	0.34	463	0.38	1,084	0.32	1,004	0.31
Total study area	574	0.34	770	0.35	1,569	0.30	1,402	0.29
Pacific white-sided dolphin								
Northern	1,215	0.69	532	1.04	628	1.05	2,345	0.58
North central	3,427	0.50	5,281	0.40	10,838	0.45	1,580	0.58
South central	2,828	0.46	1,553	0.70	10,174	0.56	2,628	0.50
Offshore	2,152	0.90	5,810	6.26	8,500	0.51	5,424	0.82
Inshore Stratum	7,469	0.45	7,366	0.48	21,640	0.45	6,552	0.43
Total study area	9,621	0.44	13,176	0.98	30,140	0.39	11,976	0.45
Northern right whale dolphin								
Northern	1,776	0.99	219	1.02	523	0.75	493	0.74
North central	3,650	0.69	1,351	0.45	1,804	0.43	2,867	0.81
South central	3,949	0.68	1,565	0.71	4,789	0.71	4,833	0.95
Offshore	766	1.00	3,320	4.67	16,580	0.98	14,425	1.10
Inshore Stratum	9,375	0.71	3,135	0.50	7,116	0.57	8,193	0.86
Total study area	10,141	0.66	6,455	1.16	23,696	0.87	22,618	1.02

Table 2.6b (continued).

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	N	CV	N	CV	N	CV	N	CV
Killer whale								
Northern	0	0.00	0	0.00	0	0.00	12	0.90
North central	35	0.74	27	0.88	182	1.04	5	1.03
South central	0	0.00	0	0.00	0	0.00	0	0.00
Offshore	0	0.00	0	0.00	23	1.03	0	0.00
Inshore Stratum	35	0.87	27	0.95	182	1.04	18	0.77
Total study area	35	0.87	27	0.95	205	0.94	18	0.77
Sperm whale								
Northern	8	0.89	0	0.00	79	1.02	28	1.02
North central	5	0.90	0	0.00	3	1.02	28	0.47
South central	0	0.00	0	0.00	23	1.02	3	1.02
Offshore	116	0.88	0	0.00	136	1.00	99	0.52
Inshore Stratum	14	0.72	0	0.00	105	0.83	59	0.62
Total study area	130	0.87	0	0.00	240	0.70	158	0.54
Blue whale								
Northern	0	0.00	0	0.00	0	0.00	0	0.00
North central	0	0.00	0	0.00	37	0.51	3	1.02
South central	0	0.00	0	0.00	20	0.55	0	0.00
Offshore	0	0.00	0	0.00	34	0.80	0	0.00
Inshore Stratum	0	0.00	0	0.00	57	0.56	3	1.03
Total study area	0	0.00	0	0.00	91	0.52	3	1.03
Fin whale								
Northern	0	0.00	0	0.00	0	0.00	0	0.00
North central	0	0.00	0	0.00	14	0.96	8	0.63
South central	0	0.00	17	1.01	25	0.54	3	1.02
Offshore	0	0.00	0	0.00	90	0.50	0	0.00
Inshore Stratum	0	0.00	17	1.02	40	0.62	11	0.67
Total study area	0	0.00	17	1.02	130	0.55	11	0.67
Humpback whale								
Northern	0	0.00	3	1.03	10	1.03	0	0.00
North central	0	0.00	17	1.02	559	0.38	149	0.70
South central	4	1.02	67	0.62	79	0.51	8	1.02
Offshore	0	0.00	115	0.68	136	0.54	0	0.00
Inshore Stratum	4	1.03	87	0.67	648	0.53	157	0.81
Total study area	4	1.03	202	0.59	784	0.48	157	0.81

Table 2.7a. Minimum seasonal density estimates (D) and coefficients of variation (CV), by year, for selected cetacean species sighted during the MMS 1980-83 aerial surveys for the inshore stratum. Estimates do not include correction factors for perception or availability biases, $g(0)$. The total estimates for all years were calculated using standard variance-weighted formula and are thus different (i.e., generally biased high) than the inshore stratum totals presented in Table 2.6a.

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	D	CV	D	CV	D	CV	D	CV
Risso's dolphin								
1980	0.085	0.47	0.126	0.36	0.185	0.39	0.114	0.76
1981	0.050	0.42	0.039	0.43	0.150	0.36	0.079	0.62
1982	0.153	0.41	0.093	0.39	0.122	0.36	0.090	0.49
1983 (February only)	0.010	0.99	NA	NA	NA	NA	NA	NA
All years- Inshore	0.102	0.28	0.099	0.26	0.155	0.23	0.095	0.39
Dall's porpoise								
1980	0.000	0.00	0.015	0.31	0.000	0.00	0.007	0.56
1981	0.003	0.51	0.002	0.71	0.017	0.30	0.015	0.35
1982	0.022	0.27	0.007	0.43	0.029	0.24	0.027	0.26
1983 (February only)	0.017	0.55	NA	NA	NA	NA	NA	NA
All years- Inshore	0.017	0.28	0.012	0.27	0.024	0.21	0.023	0.22
Pacific white-sided dolphin								
1980	0.036	0.88	0.170	0.48	0.907	0.52	0.024	1.01
1981	0.085	0.55	0.047	0.99	0.161	0.46	0.181	0.42
1982	0.238	0.45	0.139	0.51	0.179	0.45	0.086	0.59
1983 (February only)	0.061	0.79	NA	NA	NA	NA	NA	NA
All years- Inshore	0.133	0.33	0.138	0.35	0.454	0.40	0.127	0.33
Northern right whale dolphin								
1980	0.061	0.50	0.076	0.43	0.091	0.80	0.151	0.96
1981	0.212	0.92	0.010	1.00	0.114	0.69	0.094	0.81
1982	0.161	0.55	0.060	0.80	0.131	0.46	0.151	0.87
1983 (February only)	0.121	1.46	NA	NA	NA	NA	NA	NA
All years- Inshore	0.154	0.52	0.063	0.34	0.121	0.40	0.135	0.63

Table 2.7a (continued).

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	D	CV	D	CV	D	CV	D	CV
Killer whale								
1980	0.000	0.00	0.001	0.88	0.000	0.00	0.000	0.00
1981	0.001	0.76	0.000	0.00	0.008	1.04	0.000	0.83
1982	0.000	1.01	0.000	0.00	0.000	0.00	0.000	1.04
1983 (February only)	0.000	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0.001	0.71	0.001	0.88	0.002	1.04	0.000	0.71
Sperm whale								
1980	0.000	1.24	0.000	0.00	0.000	0.00	0.000	1.00
1981	0.000	0.76	0.000	0.00	0.004	0.88	0.000	0.00
1982	0.000	1.41	0.000	0.00	0.000	0.00	0.003	0.59
1983 (February only)	0.000	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0.000	0.72	0.000	0.00	0.002	0.88	0.002	0.57
Blue whale								
1980	0.000	0.00	0.000	0.00	0.001	0.69	0.000	0.00
1981	0.000	0.00	0.000	0.00	0.000	0.63	0.000	0.00
1982	0.000	0.00	0.000	0.00	0.001	0.52	0.000	1.02
1983 (February only)	0.000	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0.000	0.00	0.000	0.00	0.001	0.43	0.000	1.02
Fin whale								
1980	0.000	0.00	0.001	1.00	0.001	0.59	0.000	1.00
1981	0.000	0.00	0.000	0.00	0.000	1.02	0.000	1.02
1982	0.000	0.00	0.000	0.00	0.000	0.81	0.000	0.75
1983 (February only)	0.000	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0.000	0.00	0.000	1.00	0.001	0.49	0.000	0.56
Humpback whale								
1980	0.000	1.01	0.002	0.82	0.002	0.51	0.001	0.63
1981	0.000	0.00	0.000	1.01	0.012	0.39	0.005	0.87
1982	0.000	0.00	0.002	0.66	0.015	0.44	0.001	0.65
1983 (February only)	0.000	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0.000	1.01	0.002	0.55	0.011	0.35	0.002	0.66

Table 2.7b. Minimum seasonal abundance estimates (N) and coefficients of variation (CV), by year, for selected cetacean species sighted during the MMS 1980-83 aerial surveys for the inshore stratum. Estimates do not include correction factors for perception or availability biases, $g(0)$. The total estimates for all years were calculated using standard variance-weighted formula and are thus different (i.e., generally biased high) than the inshore stratum totals presented in Table 2.6b.

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	N	CV	N	CV	N	CV	N	CV
Risso's dolphin								
1980	5,441	0.47	8,112	0.36	11,859	0.39	7,310	0.76
1981	3,197	0.42	2,533	0.43	9,630	0.36	5,088	0.62
1982	9,816	0.41	5,995	0.39	7,853	0.36	5,784	0.49
1983 (February only)	632	0.99	NA	NA	NA	NA	NA	NA
All years- Inshore	6,561	0.28	6,322	0.26	9,916	0.23	6,124	0.39
Dall's porpoise								
1980	0	0.00	980	0.31	0	0.00	441	0.56
1981	222	0.51	115	0.71	1,073	0.30	948	0.35
1982	1,391	0.27	418	0.43	1,868	0.24	1,704	0.26
1983 (February only)	1,087	0.55	NA	NA	NA	NA	NA	NA
All years- Inshore	1,084	0.28	754	0.27	1,562	0.21	1,456	0.22
Pacific white-sided dolphin								
1980	2,286	0.88	10,929	0.48	58,159	0.52	1,542	1.01
1981	5,423	0.55	3,040	0.99	10,300	0.46	11,592	0.42
1982	15,298	0.45	8,888	0.51	11,498	0.45	5,532	0.59
1983 (February only)	3,886	0.79	NA	NA	NA	NA	NA	NA
All years- Inshore	8,517	0.33	8,842	0.35	29,111	0.40	8,139	0.33
Northern right whale dolphin								
1980	3,907	0.50	4,889	0.43	5,849	0.80	9,714	0.96
1981	13,629	0.92	618	1.00	7,284	0.69	6,026	0.81
1982	10,308	0.55	3,868	0.80	8,378	0.46	9,673	0.87
1983 (February only)	7,756	1.46	NA	NA	NA	NA	NA	NA
All years- Inshore	9,908	0.52	4,038	0.34	7,760	0.40	8,645	0.63

Table 2.7b (continued).

Stratum	Feb-Apr		May-Jul		Aug-Oct		Nov-Jan	
	N	CV	N	CV	N	CV	N	CV
Killer whale								
1980	0	0.00	85	0.88	0	0.00	0	0.00
1981	87	0.76	0	0.00	482	1.04	22	0.83
1982	8	1.01	0	0.00	0	0.00	28	1.04
1983 (February only)	0	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	36	0.71	36	0.88	160	1.04	18	0.71
Sperm whale								
1980	20	1.24	0	0.00	0	0.00	8	1.00
1981	15	0.76	0	0.00	249	0.88	0	0.00
1982	8	1.41	0	0.00	0	0.00	183	0.59
1983 (February only)	0	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	11	0.72	0	0.00	103	0.88	119	0.57
Blue whale								
1980	0	0.00	0	0.00	73	0.69	0	0.00
1981	0	0.00	0	0.00	23	0.63	0	0.00
1982	0	0.00	0	0.00	89	0.52	9	1.02
1983 (February only)	0	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0	0.00	0	0.00	66	0.43	3	1.02
Fin whale								
1980	0	0.00	46	1.00	85	0.59	8	1.00
1981	0	0.00	0	0.00	30	1.02	7	1.02
1982	0	0.00	0	0.00	24	0.81	18	0.75
1983 (February only)	0	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	0	0.00	16	1.00	60	0.49	13	0.56
Humpback whale								
1980	20	1.01	124	0.82	97	0.51	48	0.63
1981	0	0.00	8	1.01	746	0.39	343	0.87
1982	0	0.00	120	0.66	969	0.44	92	0.65
1983 (February only)	0	0.00	NA	NA	NA	NA	NA	NA
All years- Inshore	5	1.01	99	0.55	684	0.35	123	0.66

Table 2.8. Minimum species abundance estimates, and results of significance tests for differences in seasonal abundance during the 1980-83 aerial surveys, for the total study area. Significance tests were first conducted between seasons with the greatest point differences; species with significant differences ($p \leq 0.05$) were then tested using the next greatest point difference, and repeated until no significant differences were detected. Key: n = number of sightings, N = abundance estimate (coefficients of variation for abundance estimates are provided in Table 2.6b), BCa CI(d) = BCa confidence interval (Efron and Tibshirani 1993) for the difference in abundance estimates, p-val = p-values for differences found to be significant at $\alpha \leq 0.05$. Seasons for which the comparison was made are coded as follows: (sp) spring = February-April, (sm) summer = May-July, (fa) fall = August-October, (wi) winter = November-January.

Species	Seasons	Season 1		Season 2		CI(d)		p-val
		n	N	n	N	L95%	U95%	
Risso's dolphin	sm - sp	66	10,353	54	5,636	-5,761	45,221	
Dall's porpoise	fa - sp	59	1,569	31	574	158	2,172	0.03
	fa - sm	59	1,569	28	770	-249	2,136	
Pacific white-sided dolphin	fa - sp	50	30,140	33	9,621	1,161	47,833	0.04
	fa - wi	50	30,140	24	11,976	-3,419	53,413	
Northern right whale dolphin	fa - sm	31	23,696	17	6,455	-14,096	101,534	
Killer whale	fa - wi	3	205	3	18	13	938	0.03
	fa - sm	3	205	4	27	-2	1,076	
Sperm whale	fa - sp	5	240	7	130	-344	776	
Blue whale	fa - wi	17	91	1	3	30	231	<0.001
Fin whale	fa - wi	13	130	4	11	31	320	0.003
	fa - sm	13	130	1	17	14	325	0.04
Humpback whale	fa - sp	84	784	1	4	319	1,996	<0.001
	fa - wi	84	784	13	157	20	1,840	0.05
	fa - sm	84	784	12	202	8	1,801	0.05

Table 2.9. Species seen, abundance estimates, and results of significance tests for differences in abundance for the inshore stratum between the MMS 1980-83 and SWFSC 1991-92 aerial surveys conducted during spring (Feb-April). Key: n = number of sightings, N = abundance estimate, CV = coefficient of variation for abundance estimate, CI(d) = the BCa confidence interval (Efron and Tibshirani 1993) for the difference in abundance estimates. Note: results do not allow for either perception or availability bias.

Species ¹	MMS 1980-83			SWFSC 1991-92			CI(d)	
	n	N	CV	n	N	CV	L 95%	U 95%
Risso's dolphin	51	5,237	0.42	4	16,337	0.61	-40,197	3,534
Dall's porpoise	31	574	0.34	12	1,733	0.36	-2,837	-72 *
Pacific white-sided dolphin	30	7,469	0.45	5	75,614	0.55	-162,054	549
Northern right whale dolphin	29	9,375	0.71	3	2,367	0.82	-998	26,266
Humpback whale	1	4	1.03	1	57	0.97	-207	12
Additional species (no significance tests performed):								
Common dolphin	0	-	-	2	21,926	0.80	-	-
Bottlenose dolphin	0	-	-	1	54	1.03	-	-
Killer whale	3	35	0.87	0	-	-	-	-
Sperm whale	4	14	0.72	0	-	-	-	-

* = difference is significant (p = 0.04)

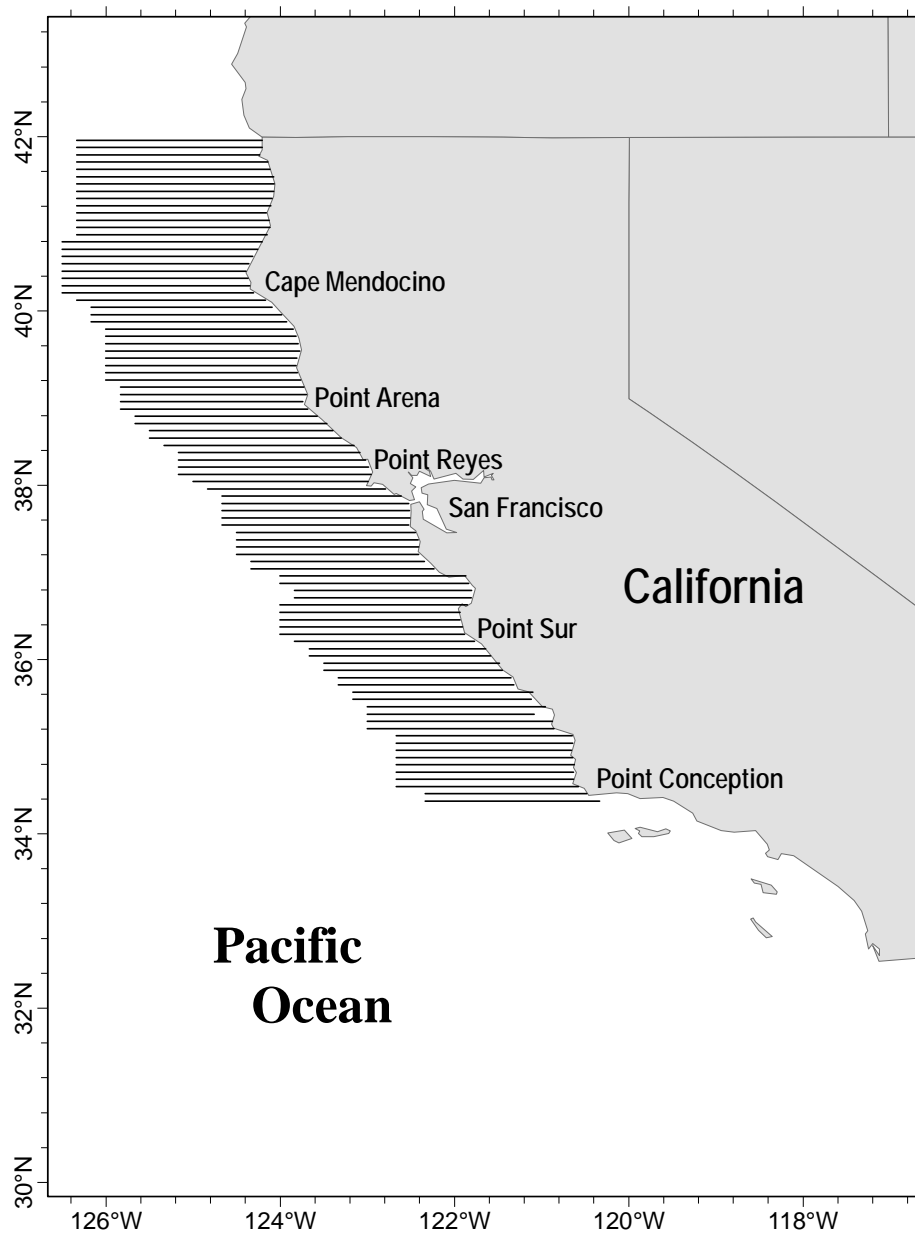


Figure 2.1. The 92 predetermined transect lines for the Minerals Management Service aerial surveys (Dohl et al. 1983). The lines were designed to survey systematically between the coast and approximately 90 nmi (167 km) offshore. Approximately 40 of the lines were surveyed monthly from March 1980 to February 1983. Scale: 1 degree of latitude = 111 km.

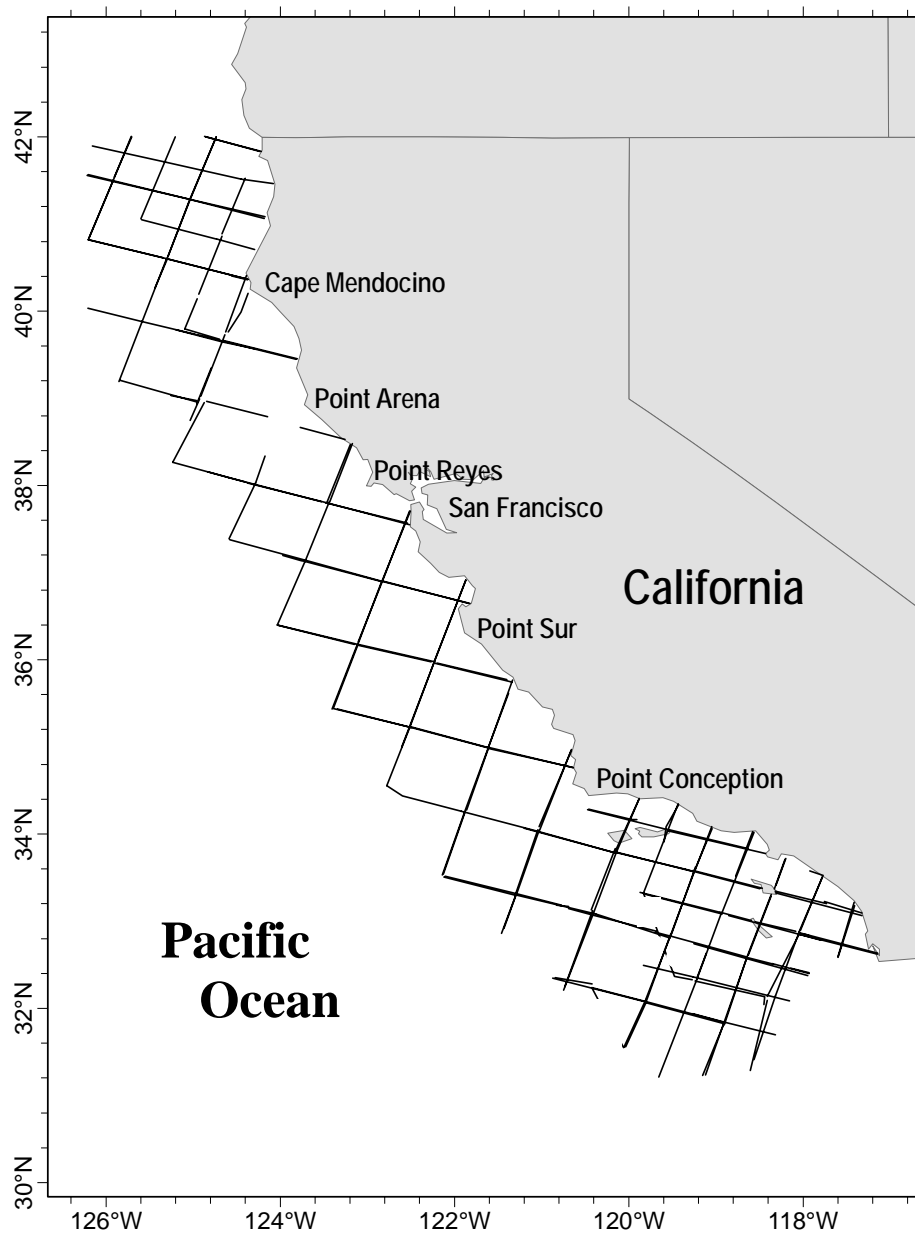


Figure 2.2. Transect lines for the National Marine Fisheries Service Southwest Fisheries Science Center aerial surveys conducted in February-March 1991 and February-April 1992 (Forney et al. 1995). The lines extended approximately 100 nmi (185 km) offshore in central and northern California and 150 nmi (278 km) offshore in southern California. Scale: 1 degree of latitude = 111 km.

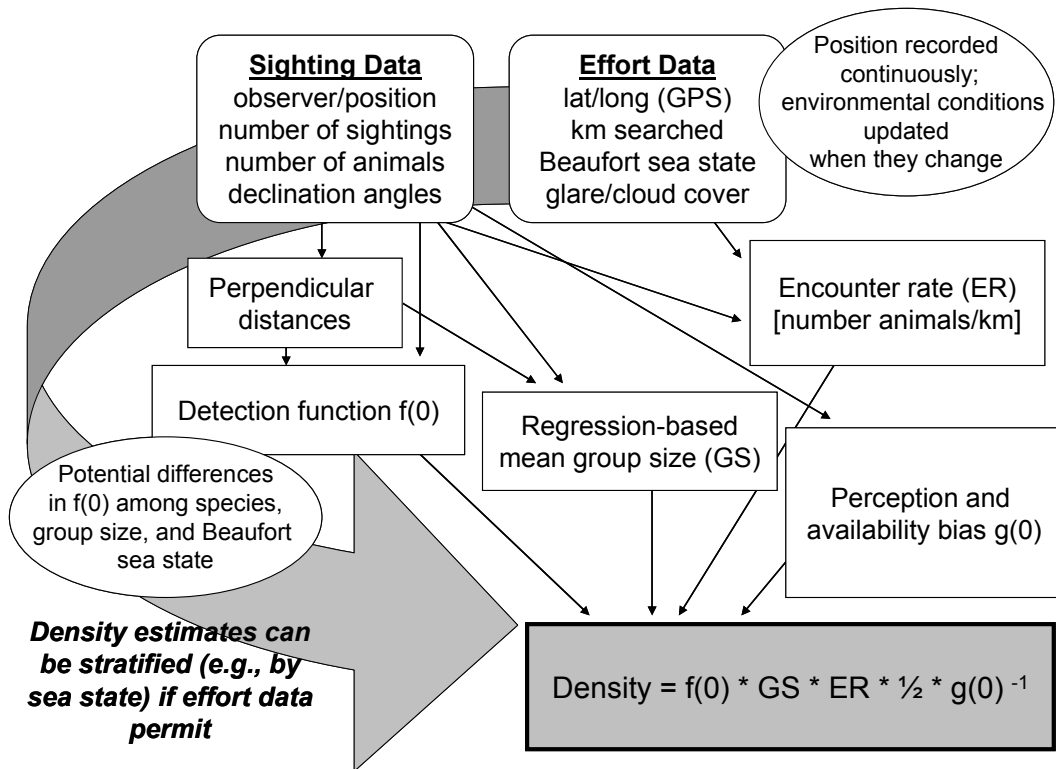


Figure 2.3a. Flow diagram of analytical steps currently used to process line-transect cetacean survey data. Note: correction factors for perception and availability biases were not incorporated into the revised 1991-92 density estimates used in this analysis.

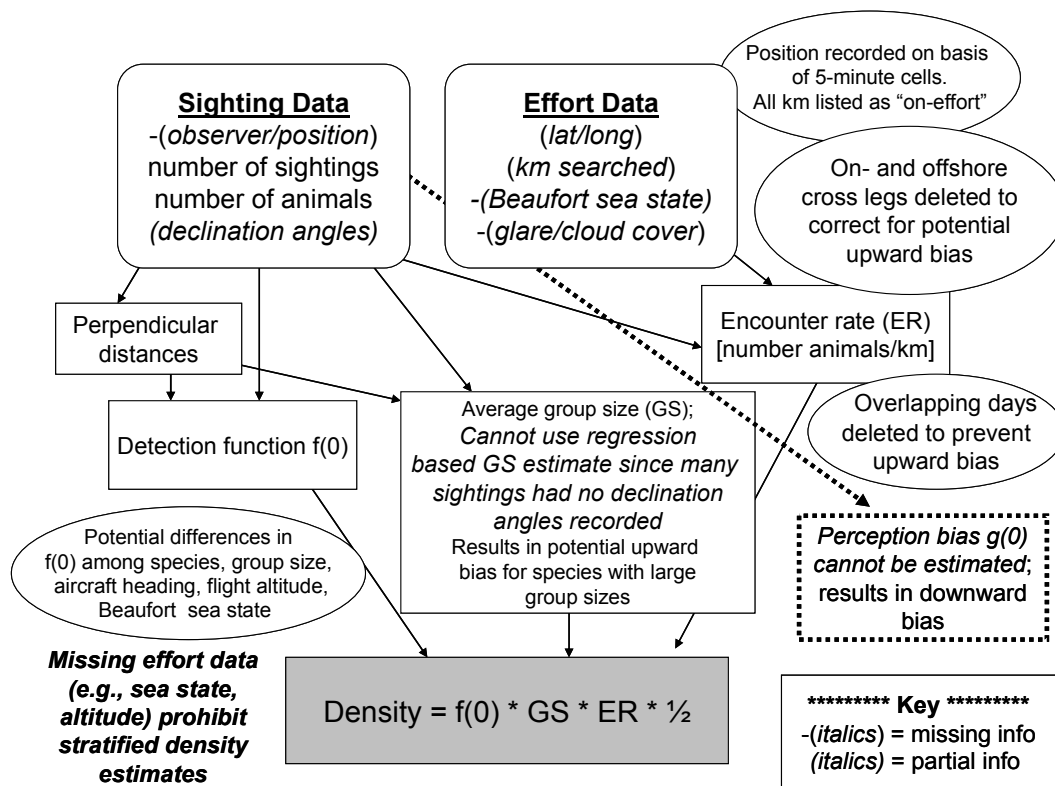


Figure 2.3b. Flow diagram of data analysis steps used to re-process MMS 1980-83 line-transect cetacean survey data. A key is included in the lower right portion of the diagram.

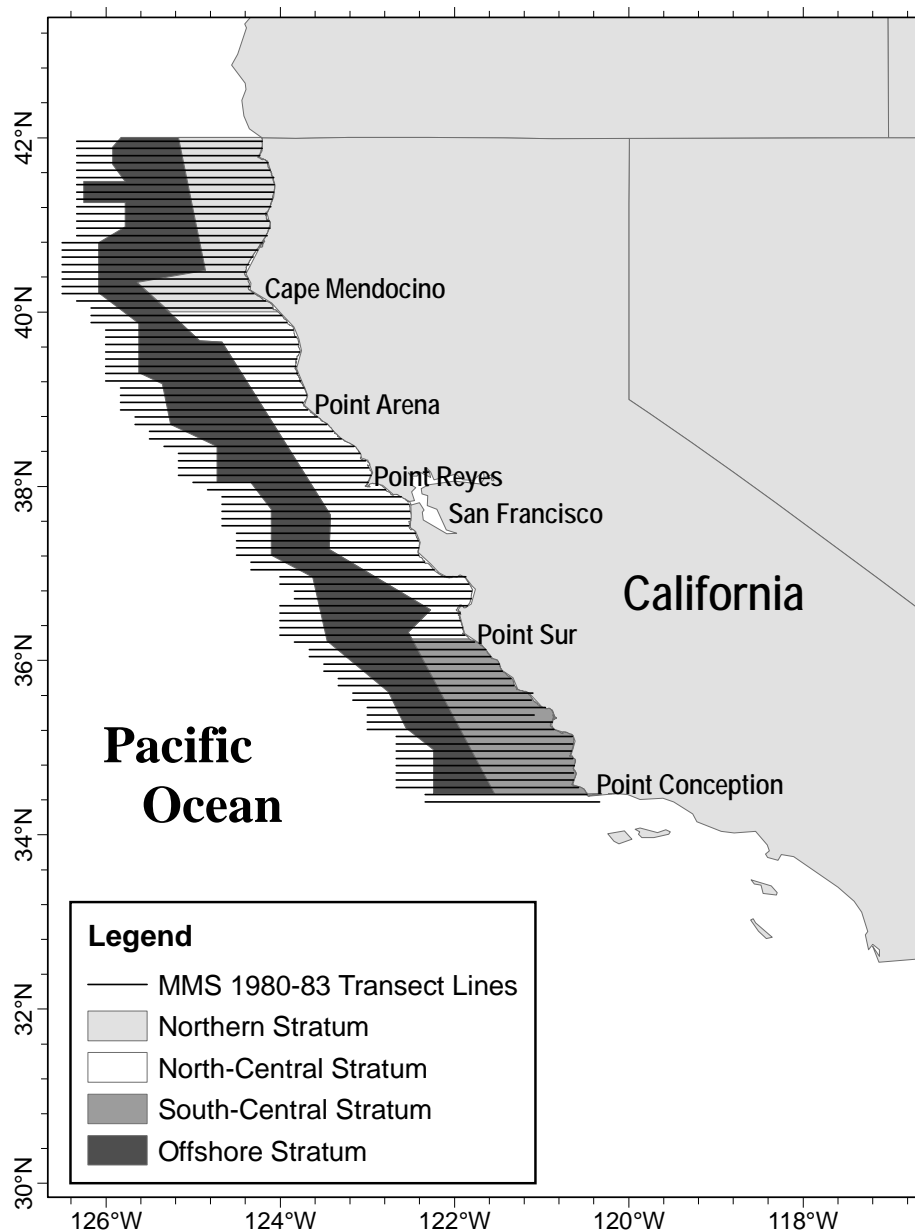


Figure 2.4. Regions used for the geographically stratified density analysis. The transect lines represent the planned survey lines for the 1980-83 aerial surveys. The offshore study boundary is represented by the offshore extent of the strata and includes the furthest distance offshore that Dohl et al. (1983) surveyed during the three-year period. Scale: 1 degree of latitude = 111 km.

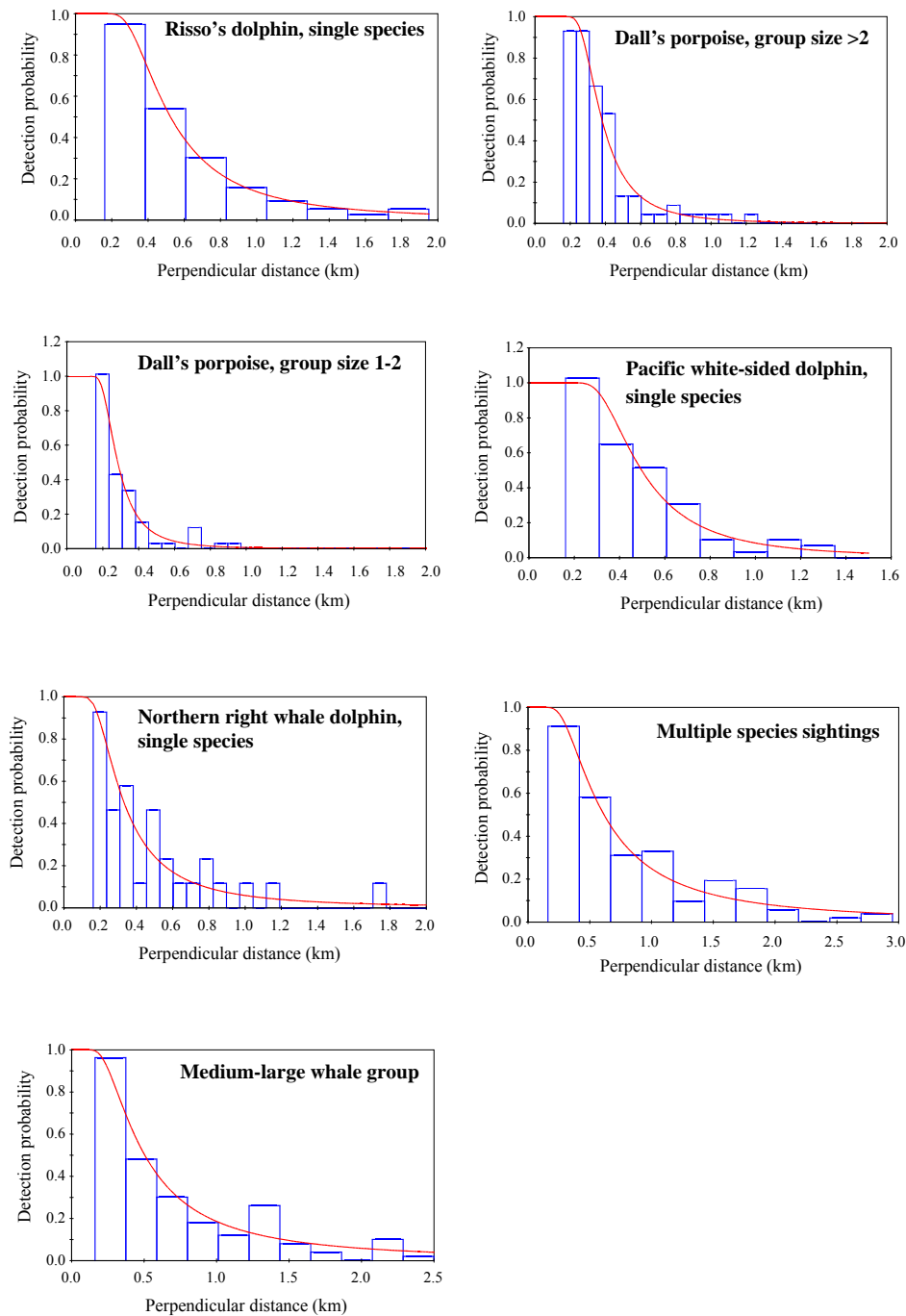


Figure 2.5. Distribution of perpendicular sighting distances and Hazard model fits for species/group categories used to analyze the 1980-83 reprocessed data. Detection probabilities are relative to the probability at the left truncation distance (162 m). Sample sizes are shown in Table 2.2.

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CHAPTER THREE

A COMPARISON OF CALIFORNIA CURRENT CETACEAN-HABITAT MODELS DEVELOPED USING *IN SITU* AND REMOTELY SENSED SEA SURFACE TEMPERATURE DATA

by

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Abstract

Generalized linear and generalized additive models were used to predict encounter rate and group size for 10 cetacean species in an approximate 818,000 km² area off California. Models were evaluated to examine the performance of remotely sensed oceanographic data compared to *in situ* measurements. In addition, performance of the two model types was compared. Cetacean sighting data were collected by the Southwest Fisheries Science Center on four systematic line-transect surveys during the summer and fall of 1991, 1993, 1996, and 2001. Predictor variables included a combination of temporally dynamic, remotely sensed environmental variables (sea surface temperature and measures of its variance) and

geographically fixed variables (water depth, bathymetric slope, and a categorical variable representing oceanic zone). The explanatory and predictive power of different spatial and temporal resolutions of satellite data were examined and included in the models on a species-specific basis. Alternative models were built using *in situ* analogs for sea surface temperature and its variance. The remotely sensed and *in situ* models with the highest predictive ability were selected based on a pseudo-jackknife cross validation procedure. Environmental predictors included in the final models varied by model, data type, and species, although overall explanatory power was similar. Satellite-derived estimates of sea surface temperature variance were found to be more effective at characterizing frontal activity due to their ability to measure heterogeneity in two dimensions. Cetacean-habitat models developed using fairly coarse-scale satellite data are shown, for most situations, to have predictive ability that meets or exceeds models developed with analogous *in situ* data, suggesting that the former could be effective tools for resource managers with access to satellite data for large regions in near real-time. The predictive ability of cetacean-environment models was affected by the level of complexity of the oceanographic environment, because more data were required to parameterize models for species that inhabit diverse environments. When sample size was small (≤ 40 sightings), the predictive power of generalized linear models built with *in situ* SST data exceeded that of the other models.

Introduction

There has been a recent increase in the development of cetacean-habitat distribution models, to improve the interpretation of abundance trends (Forney 2000), aid in the development of marine protected areas (Hooker et al. 1999; Cañadas et al. 2002), and increase understanding of cetacean-fisheries interactions (Torres et al. 2003; Kaschner 2004). Many cetacean species respond to oceanographic variability by moving over large geographical distances, and cetacean-habitat models can help distinguish apparent declines in abundance from movement of animals out of an area in response to changing oceanographic conditions (Forney 1999). In order to assess the effects of oceanographic variability on marine mammal abundance and distribution, environmental measures must be readily obtainable, ideally on a synoptic and repetitive basis, over broad ocean areas. Many of the recent quantitative analyses of species-environment relationships have been based on cetacean sighting and oceanographic data collected simultaneously from a ship (e.g., Hedley et al. 1999; Forney 2000; Ferguson et al. 2006). Satellite data typically have been used in addition to *in situ* data or when equipment failure precluded the collection of along-track data (Davis et al. 1998; Baumgartner et al. 2001; Davis et al. 2002; Hamazaki 2002). However, if remotely sensed data can be shown to be as effective at capturing species-environment relationships as *in situ* data, they could improve the utility of predictive models given their synoptic spatial coverage and near real-time availability.

In situ sea surface environmental data that can be collected while a vessel is underway (e.g., temperature, salinity, pigments) are generally available at finer spatial and temporal resolutions than satellite-derived data. *In situ* measurements of water column properties and presence of potential prey, which are generally collected on a coarser scale, are not obtainable from remotely sensed sources of data. However, shipboard surveys are expensive and, therefore, do not allow for repetitive surveys of large areas. Aerial surveys can provide a cost-effective method for surveying large areas in quick succession; however, they typically do not allow direct, *in situ* measurement of oceanographic variables. In this case, remote sensing can provide an alternate, comprehensive source of environmental data. Cetaceans do not respond directly to environmental variables that can be sensed remotely (e.g., sea surface temperature [SST]), but rather they likely respond to factors such as variations in prey distribution and availability, distribution of conspecifics (e.g., foraging or cooperative foraging), or distribution of predators. However, past studies have shown close relationships between cetacean sightings and physical proxy measures such as SST and chlorophyll (Smith et al. 1986; Reilly and Fiedler 1994; Forney 1999, 2000; Ferguson et al. 2006). These correlative relationships can therefore be useful in building effective predictive models, which in turn may lead to increased understanding of the mechanisms driving cetacean-environment relationships. If effective methods that incorporate remotely sensed data can be developed, current and historical aerial survey data can be analyzed within the

context of remotely sensed environmental variables to examine trends in species abundance and distribution over broad scales and varying resolutions.

Generalized linear models (GLMs) and generalized additive models (GAMs) have been used effectively to model cetacean sighting rates (Hedley et al. 1999; Forney 2000) and cetacean density (Ferguson et al. 2006) as a function of environmental variables; however, the majority of ecological studies that provide a direct comparison of GAMs and GLMs are found in the field of vegetation science (e.g., Franklin 1998; Wilfried et al. 2003). Further, there is a lack of comparative studies evaluating two or more statistical methods applied to the same data set (Guisan and Zimmermann 2000; Wilfried et al. 2003). In this study, we developed both GAMs and GLMs to relate cetacean sighting data from shipboard surveys in the California Current region during summer and fall 1991-2001 to remotely sensed environmental data. A separate set of GAMs and GLMs was constructed by replacing the satellite data with analogous *in situ* data collected during the shipboard surveys. Models were built for 10 species with the greatest number of sightings in order to provide the most robust environmental models: striped dolphin (*Stenella coeruleoalba*), short-beaked common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), Dall's porpoise (*Phocoenoides dalli*), sperm whale (*Physeter macrocephalus*), fin whale (*Balaenoptera physalus*), blue whale (*Balaenoptera musculus*), and humpback whale (*Megaptera novaeangliae*).

The purpose of this study was fourfold: 1) to examine the most effective temporal and spatial resolutions of remotely sensed predictors for species-environment models of cetacean density; 2) to compare the predictive ability of GAMs and GLMs; 3) to compare the performance of models built using remotely sensed data to those built using analogous *in situ* data; and 4) to examine whether the patterns identified by our models are consistent with what has been described for these species from previous California cetacean-habitat studies. The 2001 survey data used in this study were previously used for a preliminary comparison of GAMs built with remotely sensed and *in situ* environmental data (Norris 2004); however, that study did not assess predictive power and has not been published.

Methods

Field methods

Cetacean sighting data used to construct the predictive models were collected off California during the summer and fall (late July through early December) of 1991, 1993, 1996, and 2001 using systematic ship-based line-transect methods (Buckland et al. 2001). Detailed descriptions of these research cruises and survey methods are available elsewhere (Hill and Barlow 1992; Mangel and Gerrodette 1994; Barlow 1995; Von Saender and Barlow 1999; Appler et al. 2004). The amount of survey effort varied among years, but transect coverage was roughly uniform throughout the study area (Figure 3.1), and cetacean data collection procedures were consistent on all surveys (Kinzey et al. 2000; Barlow and Forney

2007). In summary, two teams of three observers rotated at 2-hour intervals among starboard observer, port observer, and data recorder positions that were located on the flying bridge of the ship. The starboard and port observers searched for animals using pedestal-mounted 25x150 binoculars (“big eyes”) while the data recorder searched using unaided eye and 7x50 handheld binoculars. In addition to sighting data, changes in Beaufort sea state conditions were entered on a laptop computer connected to the ship’s navigation system. When cetaceans were detected, the ship typically diverted from the transect line to estimate group size and identify the species present. All cetaceans sighted were identified to the lowest taxonomic level possible. We used only sightings made while on systematic transect lines and identified to species for building the models.

The *in situ* sea surface temperature data used as potential predictor variables in the comparison models were collected continuously during the line-transect surveys using a thermosalinograph with sensor at 3 m depth. Details on the collection of *in situ* oceanographic data are provided by Philbrick et al. (1993, 2003).

Analytical methods

Data processing

In order to create samples for modeling, cetacean survey data from the four shipboard surveys were separated into transect segments of approximately 5 km length, corresponding roughly to the finest resolution of satellite data used for this analysis. Each continuous section of survey effort was divided into 5 km segments,

and any remaining shorter segments were randomly assigned positions along the trackline as follows: if the remaining segment was < 2.5 km, it was added randomly to one of the adjacent 5 km segments; if it was at least 2.5 km long, it was randomly assigned to a position along the trackline between the full 5-km segments. If the entire continuous effort segment was < 5 km, it was treated as a separate segment regardless of length. The resulting dataset comprised a total of 7,347 segments, with the majority (73%) equal to the target length of 5 km, 23% of 2.5-5 km or 5-7.5 km length, and a small portion (4%) less than 2.5 km long.

Sighting data were summarized for each of the 10 species and included the total number of groups sighted and average group size per transect segment. Beaufort sea state affects the probability of detecting animals (Barlow et al. 2001), and an average sea state value was included as a continuous predictor variable in our models in order to account for sighting conditions. Because the probability of detection decreases dramatically in sea states exceeding Beaufort 5 (Barlow et al. 2001), the line-transect sighting parameter estimates derived from these survey data were based on effort in Beaufort 0-5 (Barlow 2003). Therefore, for consistency, segments with average sea state values exceeding Beaufort 5 were eliminated from this analysis. Water depth in each segment was obtained from the ETOPO2 2-minute global relief data (U.S. Department of Commerce 2006), re-gridded to match the pixel resolution used for this analysis. Slope was calculated as the magnitude of the bathymetry gradient using the gradient operator tool in GMT (Generic Mapping Tools; Wessel and Smith 1998). Individual depth and slope values estimated at the

midpoint of each segment were retrieved using the “sample” tool in ArcGIS (version 9.2, ESRI, Inc.). Oceanic zone was included as a ranked categorical variable defined roughly by water depth: shelf = waters from the coast to 200 m deep; slope = waters between 200 m and 2,000 m deep; and abyssal plain = waters deeper than 2,000 m.

Remotely sensed environmental data. SST data (National Oceanic and Atmospheric Administration/National Environmental Satellite, Data, and Information Service/Pathfinder v5) were obtained via an OPeNDAP server using Matlab code that enabled remote, automated downloading of data for user-specified positions and resolutions. Mean SST values were obtained for three temporal resolutions (1-day, 8-day, and 30-day composites centered on the day of the survey) at the finest available pixel resolution (0.05 degree or approximately 5.55 km) for initial analyses. Mean values of SST also were obtained for six spatial resolutions: 1) the pixel containing the sample midpoint (1 pixel; 5.55 km box or 30.80 km²), 2) a 4-pixel box surrounding the sample midpoint (11.10 km box or 123.21 km²), 3) a 9-pixel box surrounding the sample midpoint (16.65 km box or 277.22 km²), 4) a 16-pixel box surrounding the sample midpoint (22.2 km box or 482.84 km²), 5) a 25-pixel box surrounding the sample midpoint (27.75 km box or 770.06 km²), and 6) a 36-pixel box surrounding the sample midpoint (33.3 km box or 1,108.89 km²). Coefficients of variation (CVs) of SST were calculated for the five spatial resolutions that included more than one pixel.

We initially calculated correlation coefficients between all possible combinations of the six spatial resolutions of SST data and found them highly

correlated; the lowest R^2 value of 0.98 (p-value < 0.0000) resulted from a regression of SST values extracted from the finest (1 pixel) to the coarsest (36 pixel average) resolution considered in this analysis. To select which spatial resolution of SST to include as the best predictor variable, we built separate encounter rate and group size GAMs and GLMs for each species using only one SST resolution at a time and holding sample size constant. We did not include all resolutions in any one model-building process because regression models have difficulty distinguishing between highly correlated variables. The only variables included in the list of potential predictors were SST (at a single resolution) and Beaufort sea state. Models were constructed separately for datasets that excluded one of the four survey years, respectively, and then predictions made on the year left out of the model building process to yield an average squared prediction error (ASPE; Hastie and Tibshirani 1990). ASPE values were then summed across years for each of the six spatial resolutions. Finer resolutions were more likely to result in missing SST data because of cloud cover; therefore, we selected the resolution that maximized sample size and yielded an ASPE sum within 5% of the best predictive model. This 5% margin was selected arbitrarily because ASPE is itself a random variable, dependent on the specific samples included in the dataset.

In situ environmental data. Sea surface temperature data included in this analysis were limited to measurements collected while on the systematic transect lines. We obtained average SST and CV(SST) estimates for all values within 2.775, 5.550, 8.325, 11.100, 13.875, and 16.650 km of the segment midpoints to match the

spatial resolution of our satellite data (i.e., 5.55, 11.10, 16.65, 22.20, 27.75, and 33.30 km). For the models built using *in situ* data, we used the species-specific spatial resolutions selected for the satellite data analysis to ensure that the comparison was based on the most analogous predictor variables. We also compared the satellite-derived and *in situ* measures of SST and CV(SST) by calculating correlation coefficients for each pair of values for each of the spatial resolutions.

Model structure, development, and selection

We developed both GLMs and GAMs using the same datasets in order to compare model fit and predictive power statistically, and to gain ecological insight into variables and functional forms (i.e., the relationship of the response variable to the predictor variable) included in each type of model. Separate GLMs and GAMs were constructed to explain encounter rate and group size patterns for the 10 cetacean species.

GLMs are mathematical extensions of linear models that provide a more flexible family of regression models; they allow for non-linearity and non-constant variance structures in the data (McCullagh and Nelder 1989). In a GLM, a function (the “link”) of the mean (μ) of the response variable is modeled as a sum of predictor variables (x_1, x_2, \dots, x_n) plus a constant (α):

$$link(\mu_i) = \alpha + \sum_{i=1}^n \beta_i x_i \quad (\text{Eq. 3.1})$$

Each of the predictor variables may be transformed to represent nonlinear effects according to specified parametric functions (e.g., polynomial, exponential, logarithmic). The right side of Eq. 3.1 is termed the “linear predictor” because it is linear in the parameters ($\alpha, \beta_1, \dots, \beta_n$).

GAMs are nonparametric extensions of generalized linear models, sharing many of the same statistical properties (e.g., additive) without constraining the predictor variables to enter the model as a particular parametric form. As with GLMs, a GAM is created using a link function defining the relationship between the mean of the response variable and the predictor variables:

$$\text{link}(\mu_i) = \alpha + \sum_{i=1}^n f_i(x_i) \quad (\text{Eq. 3.2})$$

The term “additive” is used to describe the specific relationship among predictor variables (right side of Eq. 3.2): functions $f(x)$, possibly nonparametric, of predictor variables are summed to obtain the predicted response values.

The encounter rate and group size GLMs and GAMs were built using the *step.gam* function in the statistical software package S-PLUS (Professional Edition Version 6.0.2, Release 1 for Windows, Insightful Corp., 2001). Following an approach developed by Ferguson et al. (2006), a stepwise forward/backward variable selection procedure was used in which the stepwise selection process occurred twice for each model in order to improve the dispersion parameter estimate used to assess the final model. Models were constructed with both linear terms and polynomials (GLMs) or smoothing splines (GAMs) having up to three degrees of freedom.

Models built with greater than three degrees of freedom add unrealistic complexity to the functions and tend to be difficult to interpret ecologically (Forney 2000; Ferguson et al. 2006).

Encounter rate models were built with the number of sightings per segment as the response variable. The length of the segment was used as an offset in the models to standardize the expected encounter rate, accounting for variable segment length. Encounter rate models were built with all segments where SST data were available for the species-specific spatial resolution selected. In order to maximize sample size for the respective remotely sensed and *in situ* models, each model was built with as many segments for which the respective SST data were available. The dispersion parameter, an unknown but constant parameter, relates the mean to the variance and is equal to one for Poisson distributions. Encounter rates with cetacean groups are count data with a large number of zeroes and are expected to follow an over-dispersed Poisson distribution. Therefore, quasi-Poisson encounter rate models were built using a log link function and a quasi-likelihood error distribution with the variance proportional to the mean (McCullagh and Nelder 1989). Group size models were built using only those segments that contained sightings. Group size models were assumed to follow a lognormal distribution and therefore were built using the natural logarithm of group size as the response variable with an identity link function (i.e., a classical linear model where the mean and the linear predictor are identical) and a Gaussian error distribution.

Following selection of the most appropriate temporal and spatial resolution of SST data (see “Remotely sensed environmental data” above), all encounter rate and group size models were built with the full suite of potential predictor variables: zone (a categorical variable), depth, bathymetric slope, SST (at the species-specific spatial resolution), CV(SST) (at the species-specific spatial resolution), and Beaufort sea state. Akaike’s Information Criterion (AIC; Akaike 1973) was initially used by *step.gam* as the basis for selecting among potential combinations of predictor variables and varying degrees of freedom. Models were constructed separately for datasets that excluded one of the four survey years, in turn. Data for 1993 were included in all model combinations because 1993 was the year with the warmest mean sea surface temperatures and was considered essential to capture the observed interannual variability in oceanographic conditions. This initial stepwise model-building process provided us with three potential encounter rate GLMs and GAMs and three potential group size GLMs and GAMs for each species and each of the two data types (i.e., satellite and *in situ*). The “best” encounter rate and group size GLMs and GAMs were then selected based on a “pseudo-jackknife” cross validation process (Hastie and Tibshirani 1990) whereby each model selected in the first phase was then re-fit to the remaining combinations of (n-1)-year datasets and its predictive ability assessed by cross validation. This process of cross validation on all model combinations produced four ASPE values for each of the two data types; the model with the lowest sum of ASPE values was selected as the best overall model. For the encounter rate models, ASPE calculations were based on Anscombe

residuals to account for the quasi-likelihood error distribution (McCullagh and Nelder 1989). In cases where the sum of the ASPE values was identical, the model that had the lower ASPE value when tested on the novel dataset was picked. This cross-validation process allows differentiation among models that have good predictive ability, and surveys that were conducted when oceanographic conditions were similar. The model selected based on the pseudo-jackknife process was then re-fitted to all four years of shipboard data to build the final predictive model.

Density (number of animals per km²) for each species was estimated by incorporating the encounter rate and group size model results into the standard line-transect equation (Buckland et al. 2001):

$$D = \left(\frac{n}{L}\right) \cdot s \cdot \frac{1}{2 \cdot ESW \cdot g(0)} \quad (\text{Eq. 3.3})$$

where

n/L = encounter rate (number of sightings per unit length of trackline in km)

s = estimated mean group size

ESW = effective strip half-width in km, or $1/f(0)$ where $f(0)$ is the probability density function evaluated at zero perpendicular distance, i.e., on the trackline

$g(0)$ = the probability of detecting a group of animals on the trackline.

To correct for the bias resulting from back-transforming the logarithmic values produced by the group size models, we used a ratio estimator (Finney 1941; Smith 1993). We relied on published values of $f(0)$ (or ESW) and $g(0)$ for each

species as estimated from the specific survey data (Barlow 2003). There are two separate components of $g(0)$, perception bias and availability bias (Marsh and Sinclair 1989). The $g(0)$ values used by Barlow (2003) accounted for perception bias for all species and availability bias for beaked whales and sperm whales. For the other species included in this analysis there is no expected availability bias during shipboard surveys, because they should surface at least once during the time it takes a ship to pass through the area in which they would be visible. In most cases the range of Beaufort sea state conditions used to estimate the original parameters matched the range included in our analysis (i.e., 0-5). However, for Dall's porpoise published $f(0)$ and $g(0)$ values were available only for Beaufort conditions of 0-2. The application of these $f(0)$ and $g(0)$ values in our study, which included sea states of 0-5, is expected to cause a downward bias in our density estimates. We constructed Dall's porpoise models using data collected in sea state conditions of 0-5 to provide a larger sample size and to ensure coverage of a larger portion of the study area. Survey effort in Beaufort conditions of 0-2 was not distributed uniformly across the study area (see Figure 2 in Barlow and Forney, 2007). We wanted to ensure that the survey data used for modeling purposes captured the range of habitat types in the study area. Published $f(0)$ and $g(0)$ values for many species were stratified by group size and, for purposes of estimating densities, we incorporated weighted $f(0)$ and $g(0)$ values based on the number of small and large groups observed during the survey.

To compare model performance by type (GAM or GLM) and data source (satellite or *in situ*), we re-fitted each of the final models to a commonly shared dataset using all segments available for the species-specific SST resolution (i.e., segments for which both remotely sensed and *in situ* data were available) and calculated ASPE for each encounter rate and group size model. In this case, predictions were based on application of the models to the data from which they were built, and thus provide an indication of explanatory power (i.e., goodness-of-fit). Encounter rate models were fitted to all segments available for the species-specific SST resolution, while group size models were fitted to only those segments containing sightings for the species of interest (i.e., consistent with the approach used for building the models). For each species, models with the best explanatory power were defined as those that minimized ASPE. Another indication of model fit, deviance, is a measure of the discrepancy between the fitted model and the data, analogous to the residual sum of squares for regression models based on the Gaussian distribution. The simplest model, the null model, contains no predictor variables and thus assigns all variation in the response variable to the random component. Explained deviance (i.e., [null deviance – residual deviance]/null deviance, typically expressed as a percentage) was calculated for each of the encounter rate and group size models.

For an additional comparison we used paired encounter rate and group size predictions from each model type (GAM/GLM) and data source (satellite/*in situ*) to estimate density by species for the total study area. For each segment, model

predictions for encounter rate and group size were made based on the environmental conditions characterizing the segment. The predicted values for encounter rate and group size were incorporated into the line-transect equation (Eq. 3.3) to produce a density estimate for each segment, weighted by segment length. The weighted $f(0)$ and $g(0)$ values (see above) were averaged over all segments on a species-specific basis and incorporated into the segment density calculations. The point density estimates were smoothed on a grid resolution of approximately 12 km using inverse distance weighting interpolation to the second power in Surfer software (version 8). Sightings from the survey data were plotted on the maps of predicted species densities to provide a means for qualitatively evaluating the models' predictive power. Finally, the density estimates for each segment were summed and the total divided by the sum of all segment lengths to calculate average species density for the study area. Although spatial patterns are lost in this metric, the study area predictions were compared to density estimates derived by standard line-transect analyses of the actual sighting data, and allowed for a comparison of predictive power between model types and data sources.

Results

Barlow (2003) provides information on the search effort, number of species sighted, and associated line-transect abundance estimates for the 1991-2001 shipboard surveys. The 10 species we used for model development were selected to maximize sample size and provide a range of known or expected habitat preferences,

group size dynamics, and presence in the study area (i.e., year-round residents vs. seasonal visitors). They included warm-temperate/tropical species (striped dolphin, short-beaked common dolphin), cold-temperate species (Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise), a cosmopolitan species (Risso's dolphin), baleen whales present year-round (fin whale) and only during summer feeding periods (blue whale, humpback whale), as well a large toothed whale species known to occur in highly variable group sizes (sperm whale). The harbor porpoise (*Phocoena phocoena*), the gray whale (*Eschrichtius robustus*), and the bottlenose dolphin (*Tursiops truncatus*) were excluded from this analysis because they typically occur within a narrow coastal band and are generally assessed using focused surveys (Forney 1999; Buckland et al. 1993; Carretta et al. 1998). Other species encountered during the surveys had too few sightings for modeling.

Temporal and spatial resolution of satellite-derived SST data

The encounter rate and group size models built using each of the three temporal resolutions (1-day, 8-day, and 30-day composites at 5.55 km/30.8 km² spatial resolution) of satellite-derived SST data enabled a comparison of sample size and predictive power. Due to persistent cloud cover off the California coast, 1-day composites lacked sufficient data to build robust models (e.g., SST data at this resolution were available for less than 15% of our 2001 dataset). The 30-day SST composites had good explanatory ability as indicated by the percent of explained deviance for each of the (n-1)-year models, which often exceeded that of models

built with 8-day composite SST data. Predictive ability, however, as evaluated by each (n-1)-year model's predictions for the year left out of model building, was poor at the coarser resolution. A correlation analysis showed high correlation between the 1-day and 8-day SST values ($R^2 = 0.96$), indicating that the 8-day composites provided adequate coverage while maintaining fairly consistent representation of average conditions on the day of the survey. Based on this evaluation, we selected 8-day running average SST composites centered on the date of each survey segment.

Of the total 7,347 segments in our dataset, more than 35% were eliminated due to missing satellite data at the finest spatial resolution (single pixel) while less than 17% were eliminated at the coarsest spatial resolution (maximum of 36 pixels). Models were evaluated using each of the six SST spatial resolutions to enable a comparison of predictive power for each of the 10 species and to maximize our sample sizes for modeling. For Risso's dolphin, smoothing functions and polynomials in the group size GAM and GLM, respectively, produced unrealistic values when trying to predict the sizes of groups observed during the 1996 survey. In that year, there was one sighting in waters of 12° C, which was colder than the minimum temperature observed in the other three survey years (14.5° C). Therefore, we restricted the models for this species to linear terms when selecting the best SST spatial resolution. Once the SST resolution was selected, polynomials and smoothing functions were allowed in the list of potential predictors for the model selection process; only one of the initial model fits was built without the 1996 data, and we wanted the models to be built with all potential predictor variables.

For three species (northern right whale dolphin, Dall's porpoise, and fin whale) the SST resolution with the highest predictive ability for the encounter rate GAM was different from that of the encounter rate GLM. In these instances, we selected the spatial resolution based on the combined sum of ASPE values from the GAMs and GLMs. For all species, ASPE values between years showed much greater variation than between SST spatial resolution, consistent with scale analyses conducted with *in situ* data in the eastern tropical Pacific (Redfern et al. *in review*). For most species, predictive ability was higher at coarser spatial resolutions (Table 3.1). Although CV(SST) values for the five potential spatial resolutions were not as highly correlated as were SST values (R^2 values ranged from 0.26 to 0.90), a similar analysis was conducted to select which resolution would be included in the list of potential predictor variables. For a few of the species such as humpback whale, the "best" CV(SST) spatial resolution was much finer than the "best" spatial SST resolution (Table 3.1). The final datasets for each species consisted of the number of segments with available SST data for each species-specific spatial resolution; for all species combined, approximately 17% more sightings were available for building the *in situ* models than for models based on remotely sensed SST (Table 3.2).

A correlation analysis of the remotely sensed and *in situ* SST data indicated fairly consistent and high correlation across all spatial scales. In contrast, correlations between CV(SST) values were weak and increased slightly with increasing spatial scale (Table 3.3).

Encounter rate and group size models

Following data processing, the lengths of the 7,347 segments in our dataset varied from 0.06 to 7.5 km, with the majority (> 73%) equal to 5 km. Encounter rate GAMs and GLMs were built using segment length as an offset to standardize the expected encounter rate, accounting for variable segment length. However, we found that the theoretical offset relationship was not valid because short segments (< 2.5 km) tended to occur in high density areas, particularly for those species that required off-effort group size estimates. To address this potential bias, we considered excluding all segments < 2.5 km long; however, excluding the short samples would eliminate much of the encounter rate signal. Given that less than 4% of the total segments used for modeling were less than 2.5 km long, the potential bias introduced was presumed to be small and we thus included all segments in our analyses, regardless of length.

Models fitted using GAMs and GLMs were similar to each other in 1) the selection of the satellite-derived SST spatial resolution, and 2) the pseudo-jackknife cross validation analyses performed for the remotely sensed and *in situ* models. In most cases the final GAM and GLM included the same variables with similar functional relationships between predictor and response variables, particularly for those variables having the greatest effect (identified by the largest change in the mean response) (Tables 3.4a and 3.4b; Appendix A). For example, for short-beaked common dolphin the encounter rate GAM and GLM built with *in situ* data (Table 3.4b, Figure 3.2) both included four predictor variables, three of which were shared

by both models (zone, SST, and Beaufort sea state), and one that varied by model type (depth vs. slope). However, the variables that differed between the GAM and GLM had very little effect on the response variable relative to the other predictors, as indicated by the fairly flat function produced by both depth (GAM) and slope (GLM) when plotted on a common y-axis scale (Figure 3.2). In both models, SST had the greatest effect on short-beaked common dolphin encounter rates, which dropped notably in water temperatures below about 16° C. The zone variable indicated more encounters with this species are expected in slope waters (200-2,000 m deep), while sea state had a minor effect on detection probability.

Variables that had the greatest effect on encounter rate across species were SST and depth. Beaufort sea state was also included in the majority of encounter rate models, confirming this variable's effect on detection probability. SST was a key variable for seven of the ten species considered in this analysis (Appendix A). For four of these species (Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise, and humpback whale), the models indicate that encounter rates are higher at relatively lower temperatures. For striped dolphin and short-beaked common dolphin, encounters are shown to increase at relatively higher temperatures. The encounter rate models for fin whale show most encounters in moderate-temperature waters (14-19° C). Depth was a key variable in the encounter rate models for six species. Encounters with four of these species (Pacific white-sided dolphin, Dall's porpoise, humpback whale, and blue whale) are shown to increase in relatively shallower waters, whereas encounters with two species (striped dolphin

and sperm whale) increase in relatively deeper waters (Appendix A). Details on each of the predictor variables and their relationship to species-specific encounter rates and group sizes are provided in the discussion section.

For species that showed variation between the two model types, the encounter rate GAMs were generally more complex, i.e., they included more terms and higher degrees of freedom, than the equivalent GLMs. The group size models typically included fewer terms than the encounter rate models and, with the exception of northern right whale dolphin, the final GAMs and GLMs built with remotely sensed data had identical predictors. Predictor variables in the group size models built with *in situ* data showed more variation between model type.

As expected, the encounter rate data were over-dispersed relative to a Poisson distribution in the majority of models. Dispersion parameters for the remotely sensed models ranged from 1.03 to 2.85 for the GAMs and 1.03 to 4.81 for the GLMs, with the exception of Pacific-white-sided dolphin (0.366 for the GAM and 0.461 for the GLM). For the encounter rate models built with *in situ* data, dispersion parameter estimates ranged from 0.869 to 3.68 for the GAMs and 0.983 to 3.68 for the GLMs; for Pacific white-sided dolphin the dispersion parameter was 0.911 for the GAM and 0.435 for the GLM.

The percentage of deviance explained by the final encounter rate models built with remotely sensed data ranged from 4% (sperm whale) to 39% (Dall's porpoise). Corresponding figures for the final group size models ranged from 1% (humpback whale) to 30% (Pacific white-sided dolphin) (Table 3.5). The explained deviance of

models built with *in situ* data ranged from 2% (sperm whale) to 38% (Dall's porpoise) for the encounter rate models and from 4% (humpback whale) to 43% (Pacific white-sided dolphin) for the group size models (Table 3.5). Model performance as indicated by ASPE differed between species both in terms of model type and data source. However, neither model type (GAM/GLM) nor data source (remotely sensed/*in situ*) consistently performed better overall (Table 3.5). For example, for the encounter rate models, ASPE values were lower for six of the GAMs and lower for eight of the GLMs (ASPE values were identical in the remaining six cases). For the group size models, ASPE values were lower for three of the GAMs and lower for four of the GLMs (ASPE values were identical in the remaining 13 cases). When comparing data source, for the encounter rate models, ASPE values were lower for ten of the models built with remotely sensed data and lower for seven of the models built with *in situ* data (ASPE values were identical in the remaining three cases). For the group size models, ASPE values were lower for nine of the models built with remotely sensed data and lower for 11 of the models built with *in situ* data. In sum, encounter rate models built with remotely sensed data showed slightly better performance (higher explained deviance and lower ASPE values) than those built with *in situ* data, while the reverse was true for the group size models.

To estimate overall density within the study area, we incorporated weighted $f(0)$ and $g(0)$ estimates based on the number of small and large groups observed during the cruises (Table 3.6). For most of the species, particularly those with the

greatest number of sightings, density estimates were similar for both GAMs/GLMs and satellite/*in situ* data (Table 3.7). However, for species with ≤ 40 sightings (Pacific white-sided dolphin, northern right whale dolphin, and sperm whale), density estimates from models built with *in situ* SST data were much closer to density estimates derived from the observed data. For those three species, GLMs did better than GAMs. Smoothed density plots for the remotely sensed and *in situ* models that had the greatest differences in predicted/observed density estimates (Pacific white-sided dolphin remotely sensed GAM and *in situ* GLM) show obvious dissimilarities, while those that differed least (Dall's porpoise GAMs) are very similar (Appendix B).

Discussion

Spatial resolutions of SST and CV(SST)

Our SST spatial resolution analysis for the satellite-derived data provides further evidence of the high level of interannual variability in the study area. ASPE values showed much greater variation between years than between SST resolutions, consistent with scale analyses conducted with *in situ* data (Redfern et al. unpublished analyses). For all species, the encounter rate and group size models showed similar functional relationships between SST and the response variables across spatial resolution. However, for the majority of species, the greatest predictive ability was observed for the coarsest SST resolution (36 pixels or approximately 1,109 km²). There is a lack of precision in both the sighting and satellite positions that may be better represented

by coarser spatial resolutions. In addition, there is a temporal offset between the ship survey and satellite data acquisition. In the study area, upwelled water is moved offshore by Ekman transport and south by the California Current, which has a surface velocity of approximately 9 cm/second (Lynn and Simpson 1987). The spatial displacement of surface water is thus on the order of 10 km per day. A particle of water could travel 40 km over the temporal resolution (8-day composites centered on the day of the survey) used in this study.

Ecologically it is reasonable that highly mobile species such as cetaceans are filtering out finer resolution “noise” and responding to broad-scale patterns in SST and other environmental factors. These findings are consistent with results from a scale analysis of cetacean habitat models for the eastern tropical Pacific. In those models, which used *in situ* environmental data, model fit was best with 160 km spatial resolution, the largest resolution considered (Redfern et al. *in review*). Future analyses using satellite data should investigate the predictive power of spatial resolutions greater than those used here.

The predictive ability of different spatial resolutions of satellite-derived CV(SST), which we used as a proxy for frontal regions, was more variable than that of SST. For many species, the best CV(SST) spatial resolution was among the finer resolutions considered in this study (Table 3.1), perhaps reflecting the importance of localized upwelling events or small-scale frontal features.

Model performance

For each of the 10 species considered in this analysis, we evaluated the performance of four models (an encounter rate GAM and GLM and a group size GAM and GLM) built with two types of SST data (remotely sensed and *in situ*), for a total of eight models per species. To assess model performance, we examined explanatory power (based on explained deviance and ASPE) and predictive power (based on a comparison of predicted to observed density estimates). We also examined whether the distribution patterns identified by the models (based on key variables and their functional forms) were consistent with what has been described for these species from previous studies. We define a key predictor variable as one that has a large effect on the response variable relative to the other predictors, evident by large changes in the mean response over the range of the variable. (The GAM and GLM plots included in Appendix A are, for each species and each encounter rate and group size model, all plotted on a common y-axis scale. Each scale is relative to the variable having the largest y-axis range that was not influenced by a small number of outlying points. Non-key variables have slopes that approach zero.)

Explanatory power. The explanatory power of our encounter rate and group size GAMs and GLMs was very similar, and overall results were comparable for the two model types (Table 3.5). Our results are consistent with those of Franklin (1998), who found that GAMs and GLMs had similar accuracy when used to predict

the distribution of shrub species in southern California. GAMs are less restrictive than GLMs, and their use in ecological studies has increased with the recognition that species abundance should not be expected to vary linearly or monotonically with habitat gradients (Austin 2002; Oksanen and Minchin 2002). GAMs allow the data to dictate the form of the relationship between the response and predictor variables, which can be advantageous when investigating ecological relationships (Forney 2000). However, GAMs are often more difficult to interpret than GLMs and the shape of the smoothed GAM must be assessed subjectively. By restricting our level of smoothing to three degrees of freedom, we found that the functional forms of the variables selected by model type were relatively consistent. Further, based on thorough investigations of our data, we believe that three degrees of freedom are sufficient to capture the ecologically relevant patterns in the data (Forney unpublished analyses; Ferguson et al. *in prep.*).

Models built with remotely sensed and *in situ* measures of SST and its variance also exhibited similar explanatory performance as evident from a comparison of explained deviance and ASPE (Table 3.5). As noted above for the GAM and GLM comparison, there were some differences for some species, but performance was not consistently better for models built with one of the data sources. Overall, encounter rate models built with remotely sensed data tended to have lower ASPE values on a species-by-species basis, while models built with *in situ* data tended to have lower ASPE values for the group size models.

SST. SST was a key variable in the encounter rate models that explained the most deviance (> 15%), i.e., those for the Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise, and humpback whale. (Table 3.5 shows the proportion of deviance explained by each model, and Table 3.4 shows the variables included in each model; Appendix A shows which of those variables were key variables.) In all models for a given species that included SST, the basic functional form of the variable was similar between both model type (GAM/GLM) and data source (remotely sensed/*in situ*). This was not surprising given the correlation between remotely sensed and *in situ* SST values. These results indicate that remotely sensed measures of SST can be used effectively in place of *in situ* measures in GAMs and GLMs and achieve fairly consistent results.

CV(SST). There was a relatively weak correlation between the remotely sensed and *in situ* values of CV(SST) at larger spatial scales and essentially none at smaller scales (Table 3.3). This difference is likely due to the different dimensions over which SST variation was calculated: *in situ* variation was calculated from along-track SST measures, reflecting a roughly linear change (one dimensional variation), while remotely sensed measures reflect two-dimensional variation at the various spatial scales. This difference was most apparent in the group size models for the fin whale, where the functional form of CV(SST) at the 16.65 km spatial resolution differed between *in situ* and remotely sensed models. For the portion of the function where the standard error was smallest, the *in situ* models showed group size increasing as SST variation decreases. In contrast, the remotely sensed models

predicted an almost linear increase in group size with increasing SST variation, suggesting that fin whales congregate at localized frontal regions. Models built with remotely sensed data had lower ASPE values and better predicted/observed density ratios than the models built with *in situ* data, suggesting that remotely sensed data may be better suited for characterizing frontal activity (for further discussion see “fin whale” in the following “Distribution Patterns” section).

Zone and Depth. We considered zone as a potential predictor in both the encounter rate and group size models to investigate whether a categorical variable representing broad oceanographic regions was more effective at capturing species distribution patterns than a continuous depth variable. Results were mixed for both model type and data source, as some of the final models included zone, some included depth, and others included both. We found that, while the zone variable sometimes was an effective predictor (see “blue whale” in the following section), it was not consistently better than depth alone. When final models included both depth and zone as predictors, due to their correlation, in some cases one of the variables appeared to be included as noise. For example, the Dall’s porpoise encounter rate GAM built with remotely sensed data included depth, indicating that most encounters were in waters less than 2,000 m deep (Appendix A). This result was consistent with Dall’s porpoise encounter rate models built with *in situ* data (Forney 2000). However, our remotely sensed GAM included zone in addition to depth, and zone appeared to show the opposite effect on the response variable (i.e., highest encounters in waters deeper than 2,000 m). It is notable that during the stepwise

model building process, depth was the second variable to enter the model, and helped to capture much of the explained deviance (i.e., the difference in AIC = 68.478 when depth entered the model). In contrast, zone was the last variable to enter the model and explained very little deviance compared to the same model with zone excluded (i.e., the difference in AIC = 0.007). It is possible that in some cases a second variable that indicates an opposite trend can be meaningful and suggest that the functional form for the first variable needs amendment. However, in this case the AIC values are not significantly different with the inclusion of the zone variable, and based on AIC we might choose to keep zone out of the model. Regression models have problems distinguishing between effects of highly correlated variables, and in these instances it is crucial to examine results with caution.

Slope. Bathymetric slope was included in the encounter rate and group size models for some species, but it was not a key variable in any model. These results differ from those of past studies that found relationships between cetaceans and bathymetric slope (Hui 1979; Baumgartner 1997; Baumgartner et al. 2001). The difference in results may be attributable to among-study differences in scale, as model results often are dependent on the scale at which data are collected and analyzed (Wiens 1989).

Beaufort Sea State. The prevalence of Beaufort sea state in many of the encounter rate and group size models highlights the importance of accounting for environmental effects on the detectability of cetaceans. This was clearly evident in the Pacific white-sided dolphin models, where inclusion of Beaufort sea state

increased model predictive performance (see “Predictive Power”). Future research should investigate whether the inclusion (either in the encounter rate or the sighting parameter models) of other factors known to affect the likelihood of detecting cetaceans, e.g., glare, visibility, etc. (Barlow et al. 2001), might improve the predictive performance of habitat models.

Predictive Power. True predictive power only can be evaluated using independent data, i.e., not used in constructing the models. However, the pseudo-jackknife cross validation process we used to build and select models inherently provided a measure of prediction, because one year was treated as “novel” in each of the jackknife iterations. We also assessed predictive performance by comparing our model-based density predictions to density estimates derived from conventional line-transect analyses. The model-based density predictions were calculated based on the combined predictions from the respective encounter rate and group size models, thus providing an overall evaluation of predictive performance between GAMs/GLMs and satellite/*in situ* data. In addition, our density measures were based on application of the group size models to all segments in the dataset, whereas goodness of fit of the group size models was based only on those segments used to build those models (i.e., the segments containing sightings). In general, we saw relatively good agreement between the observed and predicted values.

Density predictions for striped dolphin, short-beaked common dolphin, Dall’s porpoise, fin whale, blue whale, and humpback whale were very close to densities estimated directly from the sighting data. The ratio of predicted/observed

values ranged from 0.968 to 1.041 with the exception of the remotely sensed GLM for short-beaked common dolphin (0.900). Also, performance was similar for GAMs vs. GLMs and remotely sensed vs. *in situ* data (Table 3.7). For all those species except striped dolphin ($n = 47$), greater than 75 sightings were used to build the models.

In contrast, all models built for Risso's dolphin exhibited poor predictive performance; predicted density estimates were greater than 27% higher than estimates from the observed data. This was consistent with the low explained deviance for both encounter rate and group size models (less than 8%). In addition to relatively small sample size ($n = 70$), each Risso's dolphin model contained only one linear predictor, with depth affecting encounters and SST affecting group size. This was the only species for which models were identical between type (GAM/GLM) and data source (remotely sensed/*in situ*). The Risso's dolphin models provided an opportunity for a direct comparison between models built with remotely sensed and *in situ* SST data; while both over-predicted density relative to the density estimate based on the observed data, predictions based on the *in situ* models were about 7% closer. The *in situ* dataset included lower temperatures than the remotely sensed measures, as evident in the Risso's dolphin group size models (Appendix A). This probably served to increase their predictive power because the models built with *in situ* data included a greater temperature range.

Models with the largest range in predictive ability were apparent from the density predictions for the three species with the fewest sightings; Pacific white-

sided dolphin ($n = 25$), northern right whale dolphin ($n = 40$), and sperm whale ($n = 37$). In all cases, density predictions derived from the *in situ* GLMs were the most similar to density estimates from the observed data. The most extreme case was for Pacific white-sided dolphin, the species with the fewest sightings available for modeling. For that species, the ratio of predicted/observed density estimates ranged from 0.43 (*in situ* GAM) to 0.968 (*in situ* GLM). This result was surprising given that explained deviance was the highest of any of the group size models, and the third highest for the encounter rate models (Table 3.5). The *in situ* GLM's superior performance relative to the other models may be due to the inclusion of Beaufort sea state as a predictor variable in the encounter rate model; it was absent from all the other encounter rate models. In addition, the increased predictive performance noted for the *in situ* GLMs relative to the other models could be due in part to the increased sample size used for building the models; for these three species, there were 23% to 39% more sightings available for building the *in situ* vs. the remotely sensed models (Table 3.2).

In addition to sample size, the predictive ability of cetacean-environment models is affected by the level of complexity of the oceanographic environment. More data are required to parameterize models for species that inhabit diverse environments. For example, despite small sample size ($n = 47$), all the models for striped dolphin had ratios of predicted to observed density estimates that approached one (Table 3.7). Striped dolphins are found in tropical and warm-temperate offshore waters (Perrin et al. 1994), and the key predictor variables included in the models,

depth and SST, captured this pattern adequately with few data. In contrast, Pacific white-sided dolphins occur primarily in shelf and continental slope waters off California that are oceanographically more complex (e.g., highly variable bathymetry, water temperature, etc.), and more data are required for model parameterization.

Data loss due to cloud cover is one of the main disadvantages associated with using satellite data from passive infrared sensors such as the Advanced Very High Resolution Radiometer (AVHRR). In the California study area, persistent cloud cover is often associated with coastal upwelling areas in summer, indicating that models built with remotely sensed data are somewhat habitat-dependent. Satellite-derived SST data were available for only 67% of the database segments that included sightings of Dall's porpoise (Table 3.2), a species known to be associated with coastal, upwelled water (Forney 2000 and this study). In contrast, these data were available for 80% of the segments containing sightings of the short-beaked common dolphin, a species associated with warmer, offshore water (Forney 2000 and this study).

Distribution patterns

To assess the ability of the models to identify species-environment relationships that are consistent with known distribution patterns, key variables and their functional forms are discussed separately for each species below. Maps of predicted species densities and actual sighting locations provide a visual

representation of each model's ability to capture the spatial distribution pattern of each species (Appendix B).

Striped dolphin. Despite relatively low explained deviance in the models for striped dolphin (Table 3.5), the density predictions for this species were all very close to the observed density estimate (Table 3.7). This result is similar to that from a study using GAMs to estimate striped dolphin densities in the western Mediterranean (Gomez de Segura 2007). Inspection of the final models for this species revealed that the functional forms of key variables are consistent with known distribution patterns. As noted above, striped dolphins are found in tropical and warm-temperate offshore waters (Perrin et al. 2004), and the key predictor variables included in the models, depth and SST, effectively predicted greater numbers of encounters and animals in relatively warm, deep waters. Smoothed density plots confirm that the models captured the spatial distribution patterns of striped dolphin in the study area (Appendix B.a).

Short-beaked common dolphin. As for the striped dolphin, the models for short-beaked common dolphin explained little deviance ($\leq 7\%$; Table 3.5), but density predictions differed from the observed density by $< 1\%$ for all models except the remotely sensed GLM (10% lower than the observed; Table 3.7). As noted previously, encounters with short-beaked common dolphin were most common in waters with temperatures $\geq 16^{\circ}\text{C}$, consistent with the warm-temperate/tropical distribution range for this species (Evans 1994). All the encounter rate models showed a "threshold effect" for SST, indicating that encounters dropped

substantially in water temperatures below about 16° C. This result varies from the linear relationship to SST that Forney (2000) found in her encounter rate GAMs built using a subset of these data (1991, 1993, and 1996 surveys). This difference may be attributable to the additional year of survey data included in our models, as well as to the pseudo-jackknife cross validation procedure we used for model building and selection. Interestingly, a positive linear relationship to SST was evident in all of our group size models for this species. Models built with additional years of data will help to resolve the finer details of this relationship.

Areas with the highest predicted densities included the Southern California Bight (SCB) and the offshore regions of the study area (Appendix B.b). Inshore waters north of Point Sur had the lowest predicted densities. All models predicted higher densities in the southern half of the study area, with decreasing densities north of about 37° N latitude (Appendix B.b). Common dolphins historically occurred primarily south of Point Conception (Dohl et al. 1986), but the 1991-2001 survey data used for this analysis include sightings of this species up to the northern extent of the study area (42° N latitude). Our models captured the seasonal shift in common dolphin distribution, with animals moving north of Point Arguello and further offshore during the summer months, as noted previously by Forney and Barlow (1998).

Previous studies have suggested that *Delphinus* spp. concentrate along areas of high relief within the Southern California Bight (SCB) (Hui 1979). In our final encounter rate models, slope was included in the *in situ* GLM for short-beaked

common dolphin (Table 3.4b), indicating a higher encounter rate in areas of steeper bathymetry; however, relative to the other predictor variables included in the model, slope had little effect (Figure 3.2.b). Differences between our results and those of Hui (1979) could be attributed to the additional variables included in our analysis (i.e., temperature and zone), which appear to have more of an effect on abundance of short-beaked common dolphins than does slope. In addition, there were differences in how slope was measured in the two studies; Hui used a categorical index with five categories of contour interval whereas we used a continuous variable. The greatest difference, however, was the extent of the study areas; our study area was broad whereas Hui analyzed data from a localized area in the SCB.

Risso's dolphin. As noted above, the models built for Risso's dolphin exhibited poor explanatory (Table 3.5) and predictive (Table 3.7) performance that may be attributed in part to the relatively small sample size ($n = 70$). Each model for this species contained only one linear predictor (Table 3.4), and models were identical between type (GAM/GLM) and data source (remotely sensed/*in situ*). Depth affected encounters (more encounters in shallow waters) and SST affected group size (larger groups in colder water). The paucity of predictor variables included in the models may also suggest that the environmental variables used in this study were not effective at capturing distribution patterns for this species. Poor model performance is clearly evident in the smoothed density plots for this species. Those show very little correlation between predicted density patterns and actual survey sightings of this species, on which the models were based (Appendix B.c).

Other studies have found Risso's dolphin to be associated with the continental slope and with regions having steep bathymetry (Dohl et al. 1978, 1983; Green et al. 1992; Baumgartner 1997, 2001); however, neither the slope nor zone variables were included in the final models for this species. Risso's dolphins are found in warm-temperate and tropical waters world-wide (Kruse et al. 1999), and have been seen off the entire U.S. west coast. There may be a shift in distribution from California during cold water months northward to Oregon and Washington in late spring and summer (Green et al. 1992). The negative relationship to SST in the group size models appears inconsistent with this species' occurrence in relatively warmer water, but it is consistent with the data used in this analysis; during the 1991-2001 surveys, larger groups were generally seen north of Point Conception where waters tend to be cooler, with smaller groups sighted more frequently in the SCB. These data indicate that group size may be affected by more complex ecological or behavioral factors that are not captured by models built with fairly broad-scale environmental predictor variables.

Pacific white-sided dolphin. The predicted/observed ratios for Pacific white-sided dolphin density in the total study area exhibited the greatest differences (0.431 to 0.968), with superior performance attributed to predictions from the *in situ* encounter rate and group size GLMs (Table 3.7). This difference in performance is not as obvious when comparing smoothed density plots for this species, as all four models appear to capture the general distribution patterns of Pacific white-sided dolphins in the study area (Appendix B.d). Key variables included in the encounter

rate models for Pacific white-sided dolphin were SST and either depth or zone, with more encounters predicted for cooler waters over the continental shelf and slope, consistent with known distribution patterns (Barlow and Forney 2007). The models built with remotely sensed data also included CV(SST) as a key variable, suggesting that more encounters occur in frontal regions. All group size models included Beaufort sea state, and the two *in situ* models included two additional variables, zone and CV(SST). The function of the latter variable was consistent with the remotely sensed encounter rate models, predicting larger groups in waters with higher SST variation. The zone variable, however, produced an unexpected effect as larger groups were predicted for waters deeper than 2,000 m. The variables in the *in situ* group size models (GAM and GLM) were identical, and there were similarities between most of the key variables and functions included in the encounter rate models. Therefore, the variable responsible for the superior total study area density prediction was Beaufort sea state, which was included in the encounter rate model of the *in situ* GLM. The increased predictive ability is thus not related directly to the type of SST data, but rather to the inclusion of a variable that accounted for the likelihood of detecting groups of the animals.

Northern right whale dolphin. For this species, the effect of CV(SST) on group size was consistent between the remotely sensed and *in situ* models, as both indicated greater numbers of animals in waters with higher SST variation (frontal regions). Northern right whale dolphins feed primarily on mesopelagic fish and squid, and are known to occur frequently with other cetaceans, particularly Pacific

white-sided dolphins (Jefferson et al. 1994). Interestingly, CV(SST) was also included in the remotely sensed encounter rate models and *in situ* group size models for Pacific white-sided dolphin, with a similar effect (more frequent encounters and larger groups in regions with greater SST variation). All the encounter rate models for northern right whale dolphin showed a “threshold effect” for SST, indicating that encounters dropped substantially in water temperatures greater than about 16° C. This result is consistent with this species’ tendency to occur in relatively colder waters off California (Leatherwood et al. 1982; Jefferson et al. 2004). Regions with the highest predicted densities included inshore waters north of Point Conception, with the greatest concentrations between Point Arena and Cape Mendocino (Appendix B.e). The smoothed density plots revealed differences in model predictions consistent with the predicted/observed density ratios; the GAM built with remotely sensed data (predicted/observed = 0.819) failed to predict increased relative densities in some of the offshore areas and in the SCB that were captured by the *in situ* GLM (predicted/observed = 0.957).

Dall’s porpoise. Encounter rate models for Dall’s porpoise had the highest explained deviance (> 36%), and predicted densities for this species were, for all model types, close to the density we estimated directly from the corresponding data (Table 3.7). Key predictor variables in the Dall’s porpoise encounter rate GAMs included SST, depth, and Beaufort sea state. These terms were similar in functional form to encounter rate GAMs developed for this species by Forney (2000), confirming its preference for cooler, upwelling-modified water. Regions with

highest predicted densities include inshore waters north of Point Sur (Appendix B.f). A comparison of smoothed density predictions to actual survey sightings confirm that all four models were effective at capturing the general distribution pattern of Dall's porpoise in the study area (Appendix B.f).

As expected, our application of $f(0)$ and $g(0)$ values derived for Beaufort sea states of 0-2 to effort conducted in sea states of 0-5 resulted in a substantial downward bias in our density estimates of Dall's porpoise. Our density estimates (direct or model-based) for surveys with Beaufort sea states 0-5 ($0.016 \text{ animals/km}^2$) were about 2 to 5 times lower than those estimated directly from the same surveys when only the survey coverage with Beaufort sea states of 0-2 was included (range: 0.038 to $0.086 \text{ animals/km}^2$; Barlow 2003).

Sperm whale. With the exception of the encounter rate GAM built with remotely sensed data, all the final models for sperm whale included either the zone or depth variable. Depth was included in the encounter rate GLM built with remotely sensed data and zone was included in both the encounter rate GAM and GLM built with *in situ* data (Tables 3.4a and 3.4b; Appendix A). The functional form of the depth variable in the GLM built with satellite data shows encounters increasing with increasing depth up to about 3,500 m, and then declining slightly. In the *in situ* models, highest encounters are shown in waters deeper than 2,000 m (i.e., in zone 3). This species' apparent preference for deep waters is consistent with past observations (Leatherwood et al. 1982). This distribution pattern also is consistent with survey data collected monthly in the study area north of Point Conception

during 1980-83: the majority of the 67 sperm whale sightings were in slope waters or deeper (Dohl et al. 1983). In the group size models, zone was the only variable in the GAM and GLM built with remotely sensed data and depth appeared in the GAM and GLM built with *in situ* data (Tables 3.4a and 3.4b; Appendix A). All the group size models suggest that larger groups occur in deeper waters; however, this could be an artifact of the small number of sightings ($n = 2$) in waters less than 2,000 m deep. Sperm whales occur in highly variable group sizes of one (often a solitary male) up to 50 or more (Leatherwood et al. 1982). Sample size permitting, future analyses should examine whether solitary individuals occupy different habitats than the larger groups of animals.

The encounter rate GLM built with remotely sensed data and the group size GLM built with *in situ* data show negative linear relationships with SST and CV(SST). These results suggest more encounters and larger groups in cooler waters with little temperature variability. Sperm whales are widely distributed in the eastern North Pacific but they are most abundant in waters with temperatures greater than 15° C (Rice 1989). They are found year-round off California (Dohl et al. 1983; Barlow 1995; Forney et al. 1995) and are found off Oregon and Washington during the warmer seasons (Green et al. 1992). Our model results suggest that during the summer/fall months when the survey data were collected, sperm whales tended to occur in relatively cooler waters of the study area, and did not congregate near frontal regions. The smoothed density plots for this species show a lack of correlation between predicted density patterns and actual survey sightings of this

species (Appendix B.g). The failure of the models to capture the spatial distribution pattern for this species may be attributed in part to the small sample size available for model development ($n = 37$).

Fin whale. As compared to other species of baleen whales, fin whales are versatile feeders that are known to consume krill, herring, pollock, capelin, lanternfish, and occasionally squid (Leatherwood et al. 1982). This diversity in prey preference makes it difficult to interpret which group size model is more consistent with known distribution patterns. The group size models built with remotely sensed CV(SST) data suggest that fin whales congregate in frontal regions, while the *in situ* models suggest otherwise. Aggregations of fin whale have been observed year-round in central/southern California, with an increase in numbers in summer and fall (Forney and Barlow 1998). The variables and functional forms included in the encounter rate models for this species were very similar for both model types and both data sources. The key variables were zone, with most encounters over the continental slope, and SST, with most encounters in moderate-temperature waters (14-19° C, maximal at about 16-17° C). Although the encounter rate models were similar, results from both the ASPE (Table 3.5) and density (Table 3.7) comparisons suggest that the models using remotely sensed data are more accurate, implying that fin whales congregate in waters with high SST variation. This result is consistent with that of Doniol-Valcroze et al. (2007), who found high correlations between the distribution of fin whales and thermal fronts in the Gulf of St. Lawrence. This

suggests that our remotely sensed CV(SST) measures were more effective at characterizing frontal regions than our *in situ* CV(SST) measures.

The increased predictive ability of the models built with remotely sensed data is evident in the smoothed density plots for this species (Appendix B.h). Based on the sighting data, all four models accurately predicted regions with the highest densities; however, the GAM built with remotely sensed data predicted relatively higher densities for many of the smaller areas offshore and north of Point Conception where sightings were made during the 1991-2002 surveys (Appendix B.h). This difference is most notable in comparisons of the remotely sensed GAM and *in situ* GLM.

Blue whale. For this species, zone was a key variable included in the final encounter rate models built using *in situ* SST data; highest encounter rates were on the shelf and slope, with encounter rate dropping significantly in waters deeper than 2,000 m (Table 3.4b; Appendix A). Similarly, for the encounter rate models built with remotely sensed data, depth was included in the final GAM and GLM as a linear term that showed decreasing encounters with increasing water depth (Table 3.4a; Appendix A). Both models are consistent with what is known about this species, as blue whales feed off California in shelf and slope waters during summer and fall (roughly June through November; Calambokidis et al. 2003). The two encounter rate GAMs differed only in their inclusion of the depth variable; the *in situ* model included the categorical zone variable whereas the remotely sensed model included the continuous depth variable. Explained deviance and ASPE values for

the remotely sensed and *in situ* models were very similar (Table 3.5), while density estimates for the remotely sensed models were closer to the observed density estimate (Table 3.7). These results suggest that the zone and depth variables were equally effective as predictors, at least for these models.

Despite the overall good model performance indicated by the predicted/observed density estimates (0.999-1.041), smoothed density plots suggest that the models were not able to capture the spatial distribution patterns of blue whales in the study area (Appendix B.i). As noted previously, the density predictions derived for the entire study area do not provide information on how well the models captured spatial patterns. Areas with the highest predicted densities of blue whales were the shelf and slope regions along the entire coast (Appendix B.i). The failure of the models to predict areas of higher density further offshore where animals were sighted during the 1991-2001 surveys indicates that the environmental variables considered in this study did not account for the complete pattern of distribution for this species.

Humpback whale. Explained deviance was relatively high ($> 34\%$) for the humpback whale encounter rate models (Table 3.5), and predicted density estimates for this species were close to the observed for all model types (Table 3.7). Predictor variables with the largest effect on humpback encounter rates included SST and depth. Sighting rates decreased in waters warmer than about 17°C and were higher in shallow than deep waters. CV(SST) was the only predictor variable in the remotely sensed group size models, with larger groups in areas with higher SST

variation. CV(SST) spatial resolution was approximately 493 km², suggesting that this species may congregate at regional upwelling regions. Humpbacks are known to forage cooperatively, consistent with larger foraging groups in frontal areas with prey aggregations (Day 2006). Zone was the only predictor variable included in the *in situ* group size models, showing higher average group sizes in waters over the continental slope. These variables are consistent with the known distribution patterns of humpback whales off California, where they congregate to feed during spring, summer, and fall (Calambokidis et al. 2001). Regions with the highest predicted densities were inshore areas off central and, to a lesser extent, northern California, consistent with humpback whale sighting locations during the 1991-2001 shipboard surveys (Appendix B.j).

Caveats

Several sources of potential bias were associated with this analysis. Encounter rate GAMs and GLMs were built using segment length as an offset to standardize the expected encounter rate; however, we found that this theoretical offset relationship was not valid because short segments (< 2.5 km) tend to occur in high density areas, particularly for those species that require off-effort group size estimates. Options considered to address this potential bias were determined to introduce greater bias, e.g., excluding the short samples would eliminate much of the encounter rate signal. The potential effect of this bias is unclear but is presumed to

be small given that less than 4% of the total segments were less than 2.5 km long. However, this issue should be addressed in future research.

The small sample sizes used to develop many of the species models adversely affected their predictive ability. Unfortunately, species with small numbers of sightings are those for which predictive models are most needed, and conservation management decisions may need to be made on the basis of predictions from models built with few data. In this study, the models built with small numbers of sightings produced variable results across model type (GAM/GLM) and data source (remotely sensed/*in situ*) as compared to models with larger sample sizes. The latter generally exhibited good predictive performance and showed consistent results between models. For those cases where models are developed using limited sample sizes, we advocate a multiple model approach in order to compare predictions across model types. Inconsistent results suggest that data are too few to build robust models or to support reasonable predictions.

Density calculations incorporated published $f(0)$ values that were developed for truncated data (i.e., to estimate a detection function for each species group, the most distant 15% of the sightings were eliminated prior to analysis; Barlow 2003). Some of the sightings used in our models may have been beyond the truncation distance used for estimating $f(0)$, thus incorporating bias into the density estimates. Because one of our objectives was to compare the different models' predictive ability (vs. compare our density estimates to those derived using standard line-transect methods), deleting the most distant sightings prior to modeling was

considered inappropriate for this study because this would have further reduced the limited sample sizes and eliminated part of the signal. We could have truncated the sighting data prior to calculating observed densities, as perpendicular distance information for the sightings is available from the survey data. However, perpendicular sighting distances are not available for the values predicted from our models, and thus our comparison of predicted density to density estimates derived from the observations would be based on different data sets. Ideally, $f(0)$ and $g(0)$ values should be derived from the data used for modeling; however, these analyses are beyond the scope of this project and should be the focus of future work.

This analysis was based on ship survey data collected from late July through early December, with no allowance for seasonal effects within the summer/fall period or between winter/spring. Abundance and distribution patterns of the species considered could be markedly different if within- or between-season analyses were conducted. Our study benefits by having four years of data collected over a fairly wide and consistent area. However, given the high level of interannual environmental variability in the study area, the data very likely do not capture the full range of variation among (or within) years. Additional years of survey data, ideally collected year round, would help to better describe and understand cetacean distribution patterns in the study area.

Latitude and longitude were intentionally excluded from the list of potential predictor variables since we wanted to evaluate how well the models could predict patterns of cetacean distribution in a highly dynamic region. Based on the maps of

predicted species densities (Appendix B), it appears that latitude and longitude terms, as well as potential interaction terms (e.g., latitude x water depth), could account for additional variance not captured by the variables used in this analysis. Latitude and longitude interaction terms have been used effectively in predictive models (Forney 2000). However, the inclusion of latitude and longitude terms in habitat models diminishes their use for prediction in dynamic environments.

Ideally, model performance would be evaluated based on a fully-independent set of survey data. Since we had a limited number of survey years available for model development, we included measures of prediction in our model selection process; one year was treated as “novel” in each of the pseudo-jackknife iterations. We advocate an iterative process whereby future datasets are first used to validate existing models, and then included as part of the full dataset for additional model refinement.

Conclusions

The main goals of this study were to 1) examine the most effective resolutions of satellite-derived SST for cetacean-habitat models, 2) compare the predictive ability of GAMs/GLMs, 3) compare the performance of models built with remotely sensed vs. *in situ* data, and 4) examine whether the patterns identified by our models were consistent with results from past California cetacean-habitat studies. We found that, for all species, the predictive power of GAMs and GLMs showed much greater variation among years than among SST spatial resolution.

This finding emphasizes the importance of interannual variability in the study area. For most species, predictive ability was higher at the coarser spatial resolutions included in our analysis. Although results vary by species, GAMs and GLMs (both for encounter rate and group size) exhibit similar explanatory and predictive performance. If sample size is sufficient (ideally greater than 100 sightings), GAMs and GLMs built with remotely sensed measures of SST and CV(SST) can perform as well, and in some cases better, than models built with analogous *in situ* measures. It is likely that models built with remotely sensed data are more appropriate for some species than others, particularly those species that exhibit a strong association to SST (e.g., Dall's porpoise). However, additional years of data and tests on novel datasets are needed to resolve species-specific model performance.

Our study suggests that satellite-derived estimates of sea surface temperature variance are more effective at characterizing frontal activity due to their ability to measure heterogeneity in two dimensions. When sample size is limited (fewer than 40 sightings), however, GLMs built with *in situ* data appear to have better predictive power, probably reflecting the larger data sets available when there is no cloud-cover limitation. The predictive ability of cetacean-environment models was affected by the level of complexity of the oceanographic environment, because more data are required to parameterize models for species that inhabit diverse environments. Future research efforts that incorporate satellite-derived data into model predictions should consider how many data are available, particularly for those species with limited numbers of sightings. Ironically, predictive models are needed most for

those species for which the fewest sightings exist, such as beaked whales. Our limited ability to predict occurrence for these species is problematic for marine resource managers who must select minimal-impact locations for human activities that are potentially detrimental to cetaceans (e.g., Navy test and training activities).

The main disadvantage with using satellite data collected from passive infrared sensors is the potential reduction in sample size available for model building, particularly for those species known to occur in coastal upwelling regions with persistent cloud cover. This challenge can be partially overcome by averaging SST data over larger spatial resolutions, which for many species have greater predictive ability than similar data averaged over smaller spatial scales. Based on the results of this study, future research should investigate the predictive power of SST averaged over spatial resolutions greater than the maximum considered here (a six-pixel by six-pixel box using 5.55-km pixels, or 1,109 km²). The use of temporal SST composites greater than eight days also could be considered to avoid data loss. SST data obtained from microwave radiometers could help prevent data loss due to cloud cover and should be evaluated in future studies. Satellite data may never provide precise measures of water-column properties or prey indices currently available from *in situ* data; however, their repetitive and two-dimensional coverage of broad ocean areas on a near real-time basis can enable timely predictions to support resource management decisions. Since satellite data represent a grid of quantitative information, they can be used for a variety of statistical tests. Future work should focus on developing satellite-derived products that improve the

predictive performance of cetacean-habitat models, such as water mass proxies. Such variables may lead to advances in predictive modeling and provide further insight into the ecological relationships between cetaceans and their environment.

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insight and guidance throughout the completion of this analysis. Jessica Redfern provided the *in situ* data used for this project and contributed to joint discussions on modeling methodology.

Table 3.1. Summary of satellite-derived sea surface temperature (SST) and CV(SST) spatial resolutions with the greatest predictive ability for encounter rate and group size GAMs and GLMs. Numbers refer to the number of pixels included in the resolution cell. The spatial resolutions tested included 1, 4, 9, 16, 25, and 36 pixel boxes, corresponding to 5.55-33.3 km boxes (i.e., 30.8 – 1,108.9 km²).

Species	Encounter Rate		Group Size	
	SST	CV(SST)	SST	CV(SST)
Striped dolphin	36	25	36	9
Short-beaked common dolphin	36	36	36	25
Risso's dolphin	9	16	36	16
Pacific white-sided dolphin	36	9	36	9
Northern right whale dolphin	36	9	36	36
Dall's porpoise	25	36	36	36
Sperm whale	36	36	36	36
Fin whale	36	9	36	9
Blue whale	36	36	36	36
Humpback whale	36	4	36	16

Table 3.2. Number of sightings from the Southwest Fisheries Science Center's 1991, 1993, 1996, and 2001 surveys of California waters (survey) and number with known values of two potential predictors. The potential predictors are *in situ* and remotely sensed SST data (*in situ* and RS). Numbers reflect data available at the finest spatial resolution used in the encounter rate and group size models for each species (see Table 3.1). Also shown is the number of sightings for which both *in situ* and remotely sensed SST data were available (shared). The numbers reflect sightings in Beaufort sea states 0-5 that were used in this analysis.

Species	Total number of sightings			
	survey	<i>in situ</i>	RS	shared
Striped dolphin	61	60	47	47
Short-beaked common dolphin	397	394	319	316
Risso's dolphin	80	79	71	70
Pacific white-sided dolphin	41	41	25	25
Northern right whale dolphin	52	52	40	40
Dall's porpoise	268	194	179	179
Sperm whale	49	49	37	37
Fin whale	142	134	120	120
Blue whale	197	192	161	161
Humpback whale	95	95	78	78
Total	1382	1290	1077	1073

Table 3.3. Remotely sensed and *in situ* SST and CV(SST) correlations (R^2 values) at each of the spatial resolutions considered in this study. Spatial resolution indicated is for the satellite data; *in situ* values were averaged from along-track data within linear distances that matched the spatial resolution of the satellite data. CV(SST) is not applicable to the 5.55 km resolution because it includes only one pixel.

Spatial resolution	Number of pixels	SST (R^2)	CV(SST) (R^2)
30.80 km ²	1	0.81	NA
123.21 km ²	4	0.82	0.02
277.22 km ²	9	0.82	0.06
492.84 km ²	16	0.83	0.10
770.06 km ²	25	0.83	0.14
1,109.89 km ²	36	0.83	0.18

Table 3.4a. Comparison of the variables included in the final (1) encounter rate and (2) group size GAMs and GLMs built with **remotely sensed** SST and CV(SST). Linear fits are represented by “L1”. Smoothing splines (GAMs) are represented by “S#” and polynomial (GLMs) are represented by “P#”, where # is the associated degrees of freedom. Note that zone is a categorical variable. For those species where the GAM and GLM included different predictor variables and/or degrees of freedom, the variable codes are shown in bold.

(1) Encounter Rate Models

Species		Zone	Depth	Predictor Variables			Beaufort
				Slope	SST	CV(SST)	
Striped dolphin	GAM		S2		S2	L1	L1
	GLM		P2		P2	L1	L1
Common dolphin	GAM	L1			S3		L1
	GLM	L1			P3		L1
Risso's dolphin	GAM		L1				
	GLM		L1				
Pacific white-sided dolphin	GAM	L1	S3		S3	S3	
	GLM	L1	P2	L1	P3	L1	
Northern right whale dolphin	GAM	L1			S3		S3
	GLM	L1			P3		P3
Dall's porpoise	GAM	L1	S3	S3	S3	S2	S3
	GLM		P2	P3	P2		L1
Sperm whale	GAM				L1	S3	
	GLM		P2		L1	L1	L1
Fin whale	GAM	L1			S3	S2	L1
	GLM	L1			P2		
Blue whale	GAM		L1				S3
	GLM		L1				
Humpback whale	GAM	L1	L1		S3		
	GLM	L1			P3		

Table 3.4a (continued).

(2) Group Size Models

Species		Zone	Depth	Predictor Variables			Beaufort
				Slope	SST	CV(SST)	
Striped dolphin	GAM				L1	S2	
	GLM				L1	P2	
Common dolphin	GAM				L1		L1
	GLM				L1		L1
Risso's dolphin	GAM				L1		
	GLM				L1		
Pacific white-sided dolphin	GAM						L1
	GLM						L1
Northern right whale dolphin	GAM				L1	L1	
	GLM				L1	L1	P2
Dall's porpoise	GAM			L1			L1
	GLM			L1			L1
Sperm whale	GAM	L1					
	GLM	L1					
Fin whale	GAM					S2	
	GLM					P2	
Blue whale	GAM	L1		L1			
	GLM	L1		L1			
Humpback whale	GAM					L1	
	GLM					L1	

Table 3.4b. Comparison of the variables included in the final (1) encounter rate and (2) group size GAMs and GLMs built with *in situ* SST and CV(SST). Linear fits are represented by “L1”. Smoothing splines (GAMs) are represented by “S#” and polynomial (GLMs) are represented by “P#”, where # is the associated degrees of freedom. Note that zone is a categorical variable. For those species where the GAM and GLM included different predictor variables and/or degrees of freedom, the variable codes are shown in bold.

(1) Encounter Rate Models

Species		Zone	Depth	Predictor Variables			Beaufort
				Slope	SST	CV(SST)	
Striped dolphin	GAM		L1		L1		L1
	GLM		L1		L1		L1
Common dolphin	GAM	L1	S2		S3		L1
	GLM	L1		S2	P3		L1
Risso's dolphin	GAM		L1				
	GLM		L1				
Pacific white-sided dolphin	GAM	L1			S2		
	GLM		P2		L1		P3
Northern right whale dolphin	GAM	L1			S3	L1	S3
	GLM	L1			P3	L1	P3
Dall's porpoise	GAM	L1	S3	S3	S3	S3	S3
	GLM		P2		P3	P2	P3
Sperm whale	GAM	L1					S3
	GLM	L1					L1
Fin whale	GAM	L1			S3	L1	L1
	GLM	L1			P2		
Blue whale	GAM	L1					S3
	GLM	L1					P2
Humpback whale	GAM	L1	L1		S3	S3	L1
	GLM	L1	L1		P2	P2	L1

Table 3.4b (continued).

(2) Group Size Models

Species		Zone	Depth	Predictor Variables			Beaufort
				Slope	SST	CV(SST)	
Striped dolphin	GAM				L1		
	GLM				L1		
Common dolphin	GAM				L1		
	GLM				L1		
Risso's dolphin	GAM				L1		
	GLM				L1		
Pacific white-sided dolphin	GAM	L1				L1	L1
	GLM	L1				L1	L1
Northern right whale dolphin	GAM					S3	
	GLM				P2		
Dall's porpoise	GAM		S2			L1	L1
	GLM		P2			L1	L1
Sperm whale	GAM		L1		S3		
	GLM		L1		L1	L1	
Fin whale	GAM	L1				S2	
	GLM	L1				P2	
Blue whale	GAM			S3	S3		
	GLM				P3		
Humpback whale	GAM	L1					
	GLM	L1					

Table 3.5. Proportion of deviance explained (Expl. Dev.) and average squared prediction error (ASPE) for the (1) encounter rate (ER) and (2) group size (GS) GAMs and GLMs. Predictions are based on application of models to the data from which they were built, and thus provide an indication of explanatory power, i.e., model goodness-of-fit. The ER and GS model with the greatest explanatory power (as determined by lowest ASPE) for each species appears in bold. The number of samples and number of sightings reflects the numbers used to build the encounter rate models and depends on the remotely-sensed (RS) and *in situ* SST data available for the species-specific spatial resolution. The large range of ASPE values for the group size models in part reflects the range of species-specific group sizes (e.g., short-beaked common dolphins tend to occur in highly variable groups of up to thousands of animals while blue whales are usually found singly or in small groups).

(1) Encounter rate models							
Species	Number of Samples	Number of Sightings	Data	ER GAM		ER GLM	
				Expl. Dev.	ASPE	Expl. Dev.	ASPE
Striped dolphin	5500	47	RS	0.095	0.038	0.100	0.028
			<i>in situ</i>	0.057	0.032	0.057	0.032
Short-beaked common dolphin	6054	316	RS	0.046	0.185	0.048	0.187
			<i>in situ</i>	0.049	0.183	0.048	0.183
Risso's dolphin	6054	70	RS	0.053	0.056	0.053	0.056
			<i>in situ</i>	0.053	0.056	0.053	0.056
Pacific white-sided dolphin	5500	25	RS	0.319	0.118	0.279	0.102
			<i>in situ</i>	0.227	0.060	0.269	0.109
Northern right whale dolphin	6030	40	RS	0.181	0.070	0.181	0.060
			<i>in situ</i>	0.177	0.084	0.180	0.075
Dall's porpoise	5928	179	RS	0.391	0.104	0.362	0.113
			<i>in situ</i>	0.375	0.198	0.349	0.177
Sperm whale	6054	37	RS	0.044	0.079	0.053	0.070
			<i>in situ</i>	0.031	0.069	0.023	0.069
Fin whale	5500	120	RS	0.143	0.087	0.101	0.054
			<i>in situ</i>	0.131	0.093	0.095	0.064
Blue whale	6054	161	RS	0.111	0.131	0.098	0.140
			<i>in situ</i>	0.114	0.136	0.110	0.140
Humpback whale	5731	78	RS	0.340	0.093	0.319	0.108
			<i>in situ</i>	0.341	0.094	0.335	0.094

Table 3.5 (continued).

(2) Group size models							
Species	Number of Samples	Number of Sightings	Data	ER GAM		ER GLM	
				Expl. Dev.	ASPE	Expl. Dev.	ASPE
Striped dolphin	5500	47	RS	0.211	3,700	0.226	3,600
			<i>in situ</i>	0.099	3,800	0.099	3,800
Short-beaked common dolphin	6054	316	RS	0.070	52,200	0.070	52,200
			<i>in situ</i>	0.051	52,400	0.051	52,400
Risso's dolphin	6054	70	RS	0.071	531	0.071	531
			<i>in situ</i>	0.050	584	0.050	584
Pacific white- sided dolphin	5500	25	RS	0.298	18,100	0.298	18,100
			<i>in situ</i>	0.429	17,400	0.429	17,400
Northern right whale dolphin	6030	40	RS	0.152	622	0.270	654
			<i>in situ</i>	0.149	601	0.118	677
Dall's porpoise	5928	179	RS	0.031	9.32	0.031	9.32
			<i>in situ</i>	0.058	8.88	0.058	8.81
Sperm whale	6054	37	RS	0.108	59.6	0.108	59.6
			<i>in situ</i>	0.277	52.9	0.250	53.2
Fin whale	5500	120	RS	0.058	2.14	0.056	2.13
			<i>in situ</i>	0.041	2.17	0.040	2.18
Blue whale	6054	161	RS	0.079	0.747	0.079	0.747
			<i>in situ</i>	0.113	0.690	0.081	0.678
Humpback whale	5731	78	RS	0.009	2.92	0.009	2.92
			<i>in situ</i>	0.039	2.83	0.039	2.83

Table 3.6. Summary of the weighted effective strip width ($ESW = 1/f(0)$) and $g(0)$ estimates used to calculate observed and predicted densities for this analysis. The original values are those estimated from all the survey data (Barlow 2003), which included both perception and availability bias to the extent possible. These values are weighted by the number of small and large groups observed during the 1991, 1993, 1996, and 2001 surveys for the segments included in each species-specific spatial resolution.

Species	Group size	ESW		g(0)	
		original	weighted	original	weighted
Striped dolphin	1-20	0.50		0.77	
	21-100	1.24	0.913	1.00	0.883
	100+	1.84		1.00	
Short-beaked common dolphin	1-20	0.50		0.77	
	21-100	1.24	1.317	1.00	0.950
	100+	1.84		1.00	
Risso's dolphin	1-20	1.37		0.74	
	20+	2.18	1.615	1.00	0.819
Pacific white-sided dolphin	1-20	0.50		0.77	
	21-100	1.24	0.844	1.00	0.862
	100+	1.84		1.00	
Northern right whale dolphin	1-20	0.50		0.77	
	21-100	1.24	0.781	1.00	0.853
	100+	1.84		1.00	
Dall's porpoise ¹	all	0.82	0.82	0.79	0.79
Sperm whale	all	4.61	4.61	0.87	0.87
Fin whale	all	1.72	1.72	0.90	0.90
Blue whale	all	1.72	1.72	0.90	0.90
Humpback whale	all	2.89	2.89	0.90	0.90

¹The original estimates were applied to effort in Beaufort sea states 0-2; for this analysis they were applied to effort in Beaufort sea states 0-5 (density estimates are biased downward).

Table 3.7. Observed density (calculated by standard line-transect methods) and predicted density (animals per km²) based on model results. Predicted densities are based on application of the encounter rate and group size models to all segments of the datasets. The ratio of predicted/observed density appears below the predicted density estimates. The model with the ratio closest to 1/1 appears in bold.

Species	Number of Sightings	Observed density	Remotely-Sensed		<i>in situ</i>	
			GAM	GLM	GAM	GLM
Striped dolphin	47	0.0499 <i>pred/obs</i>	0.0499 0.999	0.0496 0.993	0.0483 0.968	0.0483 0.968
Short-beaked common dolphin	316	0.6726 <i>pred/obs</i>	0.6713 0.998	0.6052 0.900	0.6733 1.001	0.6737 1.002
Risso's dolphin	70	0.0172 <i>pred/obs</i>	0.0231 1.345	0.0231 1.345	0.0219 1.274	0.0219 1.274
Pacific white-sided dolphin	25	0.0350 <i>pred/obs</i>	0.0233 0.665	0.0236 0.674	0.0151 0.431	0.0339 0.968
Northern right whale dolphin	40	0.0247 <i>pred/obs</i>	0.0202 0.819	0.0205 0.830	0.0259 1.048	0.0236 0.957
Dall's porpoise	179	0.0162 <i>pred/obs</i> ¹	0.0163 1.003	0.0163 1.005	0.0163 1.003	0.0162 0.995
Sperm whale	37	0.0012 <i>pred/obs</i>	0.0010 0.793	0.0011 0.875	0.0011 0.873	0.0011 0.900
Fin whale	120	0.0028 <i>pred/obs</i>	0.0028 1.020	0.0028 1.022	0.0029 1.029	0.0029 1.029
Blue whale	161	0.0030 <i>pred/obs</i>	0.0031 1.017	0.0030 0.999	0.0031 1.041	0.0031 1.037
Humpback whale	78	0.0018 <i>pred/obs</i>	0.0017 0.978	0.0018 0.998	0.0018 0.999	0.0018 1.002

¹GAM density estimates different at 5 significant digits.

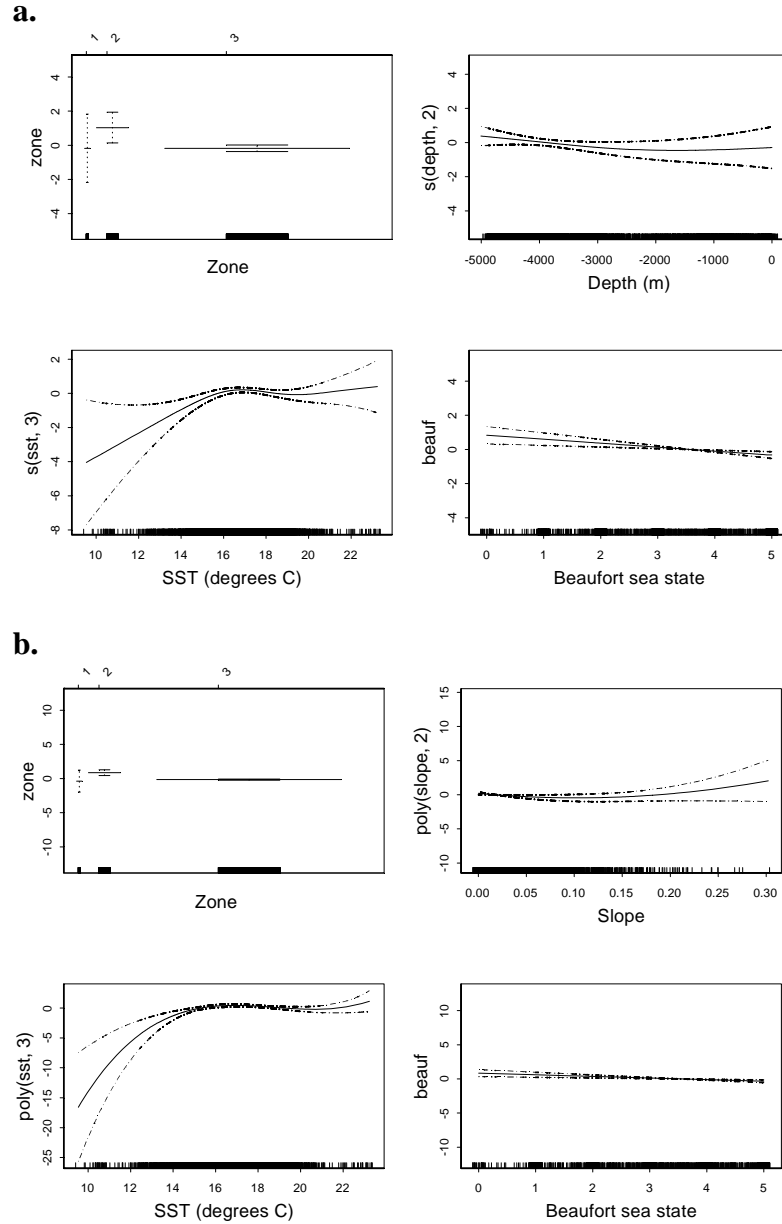


Figure 3.2. Generalized additive (a) and generalized linear (b) model functions for short-beaked common dolphin encounter rates built with *in situ* SST and CV(SST) data. Models were constructed with both linear terms and smoothing splines (s) or polynomials (poly) having up to three degrees of freedom. The y-axes represent the smoothing spline or polynomial function. Degrees of freedom for nonlinear fits are noted in the parentheses on the y-axis. Zero on the y-axes corresponds to no effect of the predictor variable on the estimated response variable (encounter rate). Functions have been scaled relative to the variable having the largest y-axis range that was not influenced by outliers. Data points for each variable are indicated by the tick marks above the x axis. The dashed lines reflect 2x standard error bands (i.e., 95% confidence interval). Zone was modeled as a categorical variable defined roughly by water depth: 1 = shelf, 2 = slope, and 3 = abyssal plain (see text for more details).

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CHAPTER FOUR

PREDICTING SEASONAL DENSITIES OF CALIFORNIA CETACEANS BASED ON MODELS BUILT WITH REMOTELY SENSED ENVIRONMENTAL VARIABLES

by

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Abstract

Seasonal variability in species distribution is a major source of uncertainty in cetacean conservation and management, and predictive models that incorporate oceanographic variability can improve our ability to identify seasonal patterns of cetacean occurrence. Generalized linear and generalized additive models were constructed to predict encounter rates and group sizes for five cetacean species in an approximate 818,000 km² area off California. Cetacean sighting data were collected by the Southwest Fisheries Science Center during four systematic ship-based line-transect surveys during the summer and fall of 1991, 1993, 1996, and 2001. Predictor variables included a combination of temporally dynamic remotely sensed environmental variables (sea surface temperature and its variance) and

geographically fixed variables (water depth, bathymetric slope, and a categorical variable representing oceanic zone). Models with the highest predictive ability were selected based on a pseudo-jackknife cross validation procedure for the summer and fall shipboard data. These models were then used to predict cetacean densities for aerial surveys conducted in winter and spring within the California study area. Predictive ability was measured in terms of the models' prediction error within and between seasons, using a nonparametric Spearman rank correlation test, as well as visual inspection of predicted and observed distributions by species. When predicting across seasons, geographic patterns of species density were captured effectively for three of the five species considered. Results indicate that interannual variability in the environmental parameters can explain some of the variation in the seasonal distribution patterns of cetaceans.

Introduction

The need for effective predictive models of cetacean occurrence and distribution has become more critical for marine resource managers who must select minimal-impact locations or seasons for an increasing number of human activities with potential to harm cetaceans (e.g., seismic surveys, Navy test and training activities, fisheries interactions, etc.). Temporal and spatial variability in species distribution and abundance remains a major source of uncertainty in managing marine resources (Ralls and Taylor 2000), particularly in regions such as the California Current where significant seasonal variation in cetacean species

distribution has been documented (Forney and Barlow 1998). To improve the predictive ability of cetacean-habitat models, it is necessary to understand more about how cetaceans respond to variability in environmental conditions on seasonal and interannual time scales. Off the California coast, the abundance of cetaceans has been estimated from shipboard line-transect surveys conducted by the Southwest Fisheries Science Center (SWFSC) during the summer and fall (henceforth referred to as 'summer' for simplicity) from 1991 to 2001, covering a total of approximately 33,000 km (Barlow 2003). Ideally, ship surveys also would be conducted during the winter and spring to provide similar cetacean sighting and corresponding environmental data for these seasons. Unfortunately, rough weather conditions make it difficult to collect shipboard line-transect data in winter and spring ('winter'), and many of the data that exist for these seasons have been collected during aerial surveys, which do not allow for the collection of complementary *in situ* oceanographic data. Aircraft-based remote sensing can supply analogous data, but in practice this is rarely done during aerial surveys of cetaceans. In addition, recent aerial survey data contain too few sightings to build and evaluate predictive environmental models.

Although the physical processes responsible for variation in local oceanographic conditions differ on seasonal, interannual, and inter-decadal time-scales, effects on sea surface temperature and other variables are similar (Chavez et al. 2003). If interannual variability in oceanographic conditions during summer is of a similar order of magnitude as seasonal variation, then it might be possible to

predict winter population densities for cetacean species that are not highly migratory based on multi-year summer models and remotely sensed oceanographic data for the winter period. Predictive cetacean models primarily have been developed using habitat data that were collected *in situ*, but Becker et al. (2007, Chapter 3) found that satellite-derived measures of SST and its variance can be effective predictors of cetacean density, thus offering a means of predicting cetacean density and distribution when only remotely sensed environmental data are available.

In many regions with strong seasonal differences (e.g., the Beaufort Sea), it would not be appropriate to build models with summer data and attempt to make winter predictions. However, in waters off California, pronounced seasonal patterns in the distribution and abundance of marine mammals have also been documented (Forney and Barlow 1998). It is possible that interannual variability in environmental conditions and cetacean distributions (e.g., caused by El Niño Southern Oscillation [ENSO] events) may be similar to seasonal variability (Forney and Barlow 1998). Coastal waters off California thus provide an appropriate study area to test the seasonal predictive power of species-environment models (i.e., building models that incorporate interannual variability in an attempt to predict seasonal distribution patterns). We developed both generalized additive models (GAMs) and generalized linear models (GLMs) to relate cetacean sighting data from shipboard surveys in the California Current region during the summer and fall from 1991-2001 to remotely sensed environmental data. The modeling framework follows that developed for a different geographic area by Ferguson et al. (2006), who

used GAMs to model cetacean density as a function of environmental variables. The resulting models are then used to predict cetacean distribution patterns based on remotely sensed environmental data for winter and spring 1991-92, a period when aerial surveys were conducted within the California study area.

Models were built for five species that are known to be present year-round and had sufficient sightings during the winter aerial surveys to evaluate the environmental models: short-beaked common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), and Dall's porpoise (*Phocoenoides dalli*). Highly migratory species such as blue whales (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) were not expected to have sufficient numbers of sightings because they are largely absent from the study area in the winter (blue whales occur from June-November and humpback whales from April-November). Gray whales (*Eschrichtius robustus*) were also excluded from the analysis since they are largely absent from the study area in the summer. The aerial survey data were used as test data to evaluate whether models constructed for summer using the extensive shipboard sighting data could predict broad distribution and density patterns during the winter period. This approach provided the advantages of a robust dataset for model construction (the shipboard data) and a test dataset during a different season for evaluation (the aerial survey data). The purposes of this study are to 1) assess whether species-environment models developed using shipboard survey data collected during

summer improve our ability to predict cetacean density for winter as compared to a “null” model (i.e., density estimates derived from summer shipboard surveys without consideration of environmental data); and 2) compare the ability of GAMs and GLMs to predict species densities across seasons. Results are examined in light of known cetacean distribution patterns documented from previous California cetacean-habitat studies.

Methods

Field methods

SWFSC California shipboard surveys

Cetacean sighting data used to construct the predictive models were collected off California by SWFSC during the summer and fall (late July through early December) of 1991, 1993, 1996, and 2001 using systematic ship-based line-transect methods (Buckland et al. 2001). Detailed descriptions of these research cruises and survey methods are available elsewhere (Hill and Barlow 1992; Mangels and Gerrodette 1994; Barlow 1995; Von Sauner and Barlow 1999; Appler et al. 2004). The amount of survey effort varied among years, but transect coverage was roughly uniform throughout the study area (Figure 4.1), and cetacean data collection procedures were consistent across all surveys (Kinzey et al. 2000; Barlow and Forney 2007). In summary, two teams of three observers rotated at two-hour intervals among starboard observer, port observer, and data recorder positions that were located on the flying bridge of the ship. The starboard and port observers

searched for animals using pedestal-mounted 25x150 binoculars (“big eyes”) while the data recorder searched using unaided eye and 7x50 handheld binoculars. In addition to sighting data, changes in Beaufort sea state conditions were entered on a laptop computer connected to the ship’s navigation system. When cetaceans were detected, the ship typically diverted from the transect line to estimate group size and identify the species present. All cetaceans sighted were identified to the lowest taxonomic level possible. To build the shipboard models, we used only sightings identified to species that were made while on systematic transect lines.

SWFSC California aerial surveys

Cetacean sighting data were collected during aerial surveys conducted by SWFSC off California in March-April 1991 and February-April 1992. Detailed descriptions of aerial survey field methods and analytical methods have been published previously (Carretta and Forney 1993; Forney et al. 1995; Forney and Barlow 1998), and pertinent aspects are summarized here. The transects followed two overlapping grids designed to survey systematically along the entire California coast out to 185 km (100 nmi) off central and northern California and 278 km (150 nmi) off southern California (Figure 4.2). However, poor weather prevented the completion of the second grid. The aerial survey study area encompassed approximately 264,000 km² of the nearshore portion of the shipboard study area. The combined transect lines were spaced approximately 41-46 km (22-25 nmi) apart, with an individual grid spacing of 82-92 km (44-50 nmi). Aircraft were outfitted

with two bubble windows for unobstructed lateral viewing and a belly port for downward viewing. The survey team consisted of three observers: two “primary” observers who searched through the left and right bubble windows and a “secondary” observer who used the belly window to search the trackline and reported sightings missed by the primary team. The field of view for the belly observer extended 55-60 degrees on each side of the aircraft, or approximately 125-150 m from the transect line at the target altitude of 213 m (700 ft). The survey team also included a data recorder who recorded sighting information and environmental conditions throughout the survey using a laptop computer connected to the aircraft’s navigation system. When cetaceans were sighted, the aircraft circled over the animals to allow observers to identify species and estimate the size of the group. All cetaceans sighted were identified to the lowest taxonomic level possible. Any additional sightings made after the aircraft had diverted from the trackline were not included in the present analysis.

Analytical Methods

We examined the predictive ability of the GLMs and GAMs using a two-step process in which 1) species-habitat models were constructed using the summer shipboard sighting data and associated environmental variables, and 2) the resulting models were used to predict cetacean encounter rates and group sizes for the winter aerial survey data (Figure 4.3). Prior to building the models, sighting and environmental data for the four shipboard surveys were separated into continuous

segments of on-effort trackline, the majority of which were 5 km long, corresponding roughly to the finest resolution of satellite data used for this analysis (Becker et al. 2007, Chapter 3). Environmental data included as potential predictor variables in the models included satellite-derived estimates of sea surface temperature (SST) and coefficient of variation (CV) of SST (to serve as a proxy for frontal regions), water depth, bathymetric slope, and oceanic zone. The latter was included as a ranked categorical variable defined roughly by water depth: shelf = waters from the coast to 200 m deep; slope = waters between 200 m and 2,000 m deep; and abyssal plain = waters deeper than 2,000 m. Beaufort sea state affects the probability of detecting animals (Barlow et al. 2001) and was included as a continuous predictor variable in our models to account for sighting conditions. Latitude and longitude were intentionally excluded from the models since our goal was to predict seasonal patterns of cetacean distribution in a highly dynamic region.

Becker et al. (2007, Chapter 3) examined the most effective temporal and spatial resolutions of remotely sensed SST and CV(SST) for species-environment models of cetacean density and selected a resolution that maximized sample size while providing species-specific models with the best predictive power. Based on their evaluation, we used 8-day running average SST composites (NOAA Advanced Very High Resolution Radiometer [AVHRR] Pathfinder v5) centered on the date of each survey segment, and obtained mean SST values and CV(SST) at the spatial resolution found to maximize predictive ability for each species (Table 4.1).

Model structure, development, and selection

Detailed descriptions of the model building and selection process can be found in Becker et al. (2007, Chapter 3), but pertinent information is summarized below.

Separate GLMs and GAMs were constructed as alternate ways to predict encounter rates and group sizes for each of the five cetacean species. Thus, there were a total of 20 models: 2 model types (GAM/GLM) x 2 dependent variables (encounter rate and group size) x 5 species. A GLM is created using a link function that defines the relationship between the mean of the response variable and the predictor variables. For each statistical distribution (e.g., binomial, gamma, Poisson) there is a specific type of link function that constrains the response variable to realistic values. For example, the number of cetacean sightings per survey segment is approximately Poisson distributed, so the log-link function is appropriate.

In a GLM, a function (the “link”) of the mean (μ) of the response variable is modeled as a sum of predictor variables (x_1, x_2, \dots, x_n), each of which may be transformed to represent nonlinear effects according to specified parametric functions (e.g., polynomial, exponential, logarithmic), plus a constant (α):

$$link(\mu_i) = \alpha + \sum_{i=1}^n \beta_i x_i \quad (\text{Eq. 4.1})$$

The right side of Eq. 4.1 is termed the “linear predictor” because it is linear in the parameters ($\alpha, \beta_1, \dots, \beta_n$).

GAMs are nonparametric extensions of generalized linear models, sharing many of the same statistical properties without constraining the predictor variables to enter the model as a particular parametric form. As with GLMs, a GAM is created using a link function defining the relationship between the mean of the response variable and the predictor variables:

$$link(\mu_i) = \alpha + \sum_{i=1}^n f_i(x_i) \quad (\text{Eq. 4.2})$$

The term “additive” is used to describe the specific relationship among predictor variables (right side of Eq. 4.2): functions $f(x)$, possibly nonparametric, of predictor variables are summed to obtain the predicted response values.

The encounter rate and group size GLMs and GAMs were built using the *step.gam* function in S-PLUS (Professional Edition Version 6.0.2, Release 1 for Windows, Insightful Corp., 2001). Encounter rate was modeled as the number of sightings per segment using all segments containing SST data for the species-specific spatial resolution, and using the length of the segment as an offset. Encounter rate data are basically count data, which are typically Poisson-distributed (Zar 1999). However, there were no sightings on the majority of the segments, so we used a quasi-likelihood error distribution with the variance proportional to the mean and a log link function (approximating an over-dispersed Poisson distribution). Group size models were built using the natural logarithm of group size as the response variable with an identity link function (i.e., a classic linear model where the

mean is equal to the linear predictor) and a Gaussian error distribution. Group size models were built using only those segments that contained sightings.

Following an approach developed by Ferguson et al. (2006), a stepwise forward/backward variable selection procedure was used in which the stepwise selection process occurred twice for each model in order to improve the dispersion parameter estimate used for the final model. Akaike's Information Criterion (AIC: Akaike 1973) initially was used by *step.gam* to select the best model at each step (see Chapter 3 for details). Models were constructed with both linear terms and polynomials (GLMs) or smoothing splines (GAMs) having up to three degrees of freedom. Models built with greater than three degrees of freedom add unrealistic complexity to the functions and tend to be difficult to interpret ecologically (Forney 2000; Ferguson et al. 2006).

The stepwise selection process was conducted separately for datasets that excluded one survey year; data from 1993 were included in all model combinations because 1993 was the year with the warmest mean sea surface temperatures and was considered essential to capture the observed interannual variability in oceanographic conditions. Cross validation (testing the predictive ability of each of the (n-1)-year models on the excluded year) provided an average squared prediction error (ASPE) for each of the (n-1)-year models selected on the basis of AIC. Each of these models was then re-fitted to the other combinations of (n-1) year datasets, a process we referred to as a "pseudo-jackknife" since it resembles the original jackknife computer-based method for estimating standard errors (Efron and Tibshirani 1998).

The models with the lowest sum of the four ASPE values produced by the pseudo-jackknife cross validation process were selected as the best encounter rate and group size GLM and GAM. ASPE calculations for the encounter rate models were based on Anscombe residuals to account for the quasi-likelihood error distribution (McCullagh and Nelder 1989). Each model selected from the pseudo-jackknife cross validation process was then re-fitted to all four years of shipboard data to build the final models.

Density estimates (number of animals per km²) were computed using the standard line-transect equation (Buckland et al. 2001):

$$D = \left(\frac{n}{L}\right) \cdot s \cdot \frac{1}{2 \cdot ESW} \quad (\text{Eq. 4.3})$$

where

n/L = encounter rate (number of sightings per unit length of trackline in km)

s = estimated mean group size

ESW = effective strip half-width in km, or $1/f(0)$ where $f(0)$ is the probability density function evaluated at zero perpendicular distance, i.e., on the trackline.

Density estimates were calculated from the survey data using standard line-transect methods in order to provide a comparison to the models' predictions. For the latter, predicted values for n/L and s were obtained from the output of the encounter rate and group size models, respectively. To correct for the bias resulting from back-transforming the logarithmic values produced by the group size models,

we used a ratio estimator (Finney 1941; Smith 1993). The probability of detecting an animal or group of animals on the transect line, $g(0)$, was not included in our density estimates. There are two separate components of $g(0)$, perception bias and availability bias (Marsh and Sinclair 1989). While correction factors for perception bias are available for many species, estimates of availability bias from aerial surveys are available for only a few species. Availability bias is more important during aerial than shipboard surveys, given the shorter time while any given part of the ocean is in view. We chose to exclude all $g(0)$ values from our density estimates since our analysis evaluated only relative patterns of predicted and observed abundance.

We relied on published values of $f(0)$ (or ESW) for each species/group size as estimated from the specific survey data (Forney and Barlow 1998; Barlow 2003). In most cases the range of Beaufort sea state conditions used to estimate the original parameters matched the range included in our analysis (i.e., 0-5). However, for shipboard sightings of Dall's porpoise a published $f(0)$ value was available only for Beaufort conditions of 0-2. The application of this $f(0)$ in our study, which included sea states of 0-5, resulted in a downward bias in our density estimates (Becker et al. 2007, Chapter 3); however, this bias is not expected to affect our comparison of relative densities.

Evaluation of model predictive ability

Differences in platform-specific biases for ship vs. aerial surveys (e.g., the proportion of diving animals missed) preclude a direct quantitative comparison of estimated densities from aerial and shipboard surveys. Consequently, to evaluate the between-season predictive ability of our final shipboard models, we used a nonparametric Spearman rank correlation test across six geographic strata. Predictive ability was based on a comparison of the models' ranked predicted values across six biogeographic strata to those derived from the actual survey data for each species' encounter rate, group size, and density (Figure 4.3). Results from the Spearman rank correlation tests were compared to results obtained when the models were used to predict densities from the shipboard survey data upon which they were built (essentially a measure of goodness of fit). In addition, results were compared to a "null" model, defined as the density derived from summer shipboard surveys without consideration of environmental data. However, given limited sample sizes and only six pairs of data available for the correlation test, statistical power is low. In addition to the rank correlation tests, we also plotted sightings from the aerial survey data on maps of predicted species densities to provide a means for qualitatively evaluating the models' predictive power.

To enable a rank analysis, we stratified the study area into six regions (Figure 4.4). Point Arguello was selected as the dividing line between the northern and southern strata because the Point Arguello/Point Conception region is a known

biogeographic boundary, marking the range limits of many marine species (Valentine 1973; Briggs 1974; Newman 1979; Doyle 1985). The northern and southern regions were further stratified consistent with the criteria used to define the categorical zone predictor variable included in the models (less than 200 m, 200-2,000 m, greater than 2,000 m). Visual inspection of survey effort plots confirmed that effort was relatively uniform within each stratum (i.e., to reduce potential bias resulting from concentrated effort in a portion of a stratum).

Published $f(0)$ values for many species were stratified by group size, because this affects the probability of detection. We used Kolmogorov-Smirnov (K-S) tests to assess whether there were regional differences in the proportion of sightings in each group size category. Our samples consisted of the number of groups in each published $f(0)$ size category in each of the six strata. Strata that revealed no significant differences ($\alpha = 0.05$) in average group size were combined in order to increase the number of sightings contributing to the weighted $f(0)$ estimates. Strata were combined and K-S tests were repeated until we had the minimum number of strata showing evidence of significant group size differences. If regional differences were identified, weighted $f(0)$ estimates were calculated for each stratum (or combined stratum) to allow for regional differences in mean group size and detection probabilities. The weighted $f(0)$ values were based on the proportion of groups within each group size range observed within each of the geographic stratum or combined geographic stratum. Weighted $f(0)$ values were computed separately for the 1991-2001 ship surveys and the 1991-1992 aerial surveys.

To qualitatively evaluate the models' predictive ability, density estimates for each segment were smoothed on a grid resolution of approximately 12 km, and the resultant predictions of distribution and density were compared with actual sightings made during the winter aerial surveys. Smoothing was done using inverse distance weighting interpolation to the second power in Surfer software (version 8). The same species-specific relative density scale was used for both the GAM and GLM to enable a comparison between model types. Models with obvious outliers were scaled so that differences in predicted densities at lower levels were visible.

Results

Barlow (2003) provides information on the search effort, number of species sighted, and associated line-transect abundance estimates for the 1991-2001 shipboard surveys. Similar information on the 1991-1992 aerial surveys is provided by Forney et al. (1995). The number of segments and sightings used to build and evaluate the predictive models also reflected the availability of satellite-derived data for each of the species-specific spatial resolutions (Table 4.2). The five species we used for model evaluation were selected based on sample size; to support a rank analysis we wanted an average of at least 2 sightings per segment (i.e., greater than 11 sightings during the aerial surveys for which SST data were available). As mentioned previously, small sample sizes combined with geographic stratification limited the power of our rank analysis. The five species used in our analysis included one warm-temperate/tropical species (short-beaked common dolphin), three

cold-temperate species (Pacific white-sided dolphin, northern right whale dolphin, Dall's porpoise), and a cosmopolitan species (Risso's dolphin). Long-beaked common dolphin (*Delphinus capensis*) cannot be reliably differentiated from the short-beaked variety during aerial surveys so predictions were made for the entire genus; however, the majority of these *Delphinus* spp. sightings likely were short-beaked common dolphins, because most of the sightings were made beyond the nearshore range of *D. capensis* (Heyning and Perrin 1994). As noted previously, highly migratory species were excluded from the analysis *a priori*. The harbor porpoise (*Phocoena phocoena*) and bottlenose dolphin (*Tursiops truncatus*) also were excluded from this analysis because they typically occur within a narrow coastal band and are generally assessed using focused surveys (Forney et al. 1991; Carretta et al. 1998). Other species encountered during the aerial surveys had too few sightings to support a rank analysis (i.e., an average of at least two sightings per stratum).

Results of the pseudo-jackknife, cross validation analyses are summarized in Becker et al. (2007, Chapter 3). For a given species, the variables and associated functional forms included in the final GAM were similar to those in the final GLM for both the encounter rate and group size models. This similarity was particularly evident for those variables having the greatest effect (identified by the largest change in the mean response) (Table 4.3; Appendix A). The weighted $f(0)$ estimates that we used to account for differences in group size in our density estimates are provided in Table 4.4.

Inspection of the last three rows of Table 4.5 indicates that for three of the five species (common dolphin, northern right whale dolphin, and Dall's porpoise), one or both models' ability to predict winter densities exceeded that of the null model. The relative abilities of GAMs and GLMs to predict ranked estimates from the novel aerial dataset varied among species, with the biggest GAM vs. GLM difference noted for Dall's porpoise (Table 4.5). Visual comparisons of predicted relative densities vs. observed sightings from the aerial surveys reveal similar differences between GAMs and GLMs (Figure 4.5); however, the smoothed density maps suggest that the predictions were better than indicated by the rank correlation tests.

Discussion

Performance of GAMs vs. GLMs

In general, GAMs and GLMs produced similar results when used for predictive habitat modeling with a few exceptions. The encounter rate GAM and GLM for northern right whale dolphin included identical terms (Table 4.3, Appendix A); however, when the polynomial SST function in the GLM was applied to the winter aerial survey data, which included colder water temperatures than the original dataset used to build the models, the fitted curve in the GLM predicted an unrealistic number of encounters (295,697). The GAM smooth function predicted high values, but, based on past survey data (Barlow 2003), these were not unrealistic (82 encounters). Overall results of the Spearman rank correlation analysis indicate that

GAMs had better between-season predictive ability than GLMs (i.e., correlation was higher for total encounter rate, group size, and density predictions; Table 4.5), due in part to the poor performance of polynomials when predicting outside of the range of values used to build the models. The apparent superior performance of the GAMs could also be due to the software platform used to build the models, as the *predict.gam* function included in S-PLUS includes a “safe prediction” algorithm (Chambers and Hastie 1991). We used the *predict.gam* function for both the GAM and GLM predictions; however, because the smoothing functions are inherently more flexible than the polynomials, GAMs are more amenable to adjustment when fitted to new data. Significant errors can result when relying on model predictions that have been extrapolated beyond the range of values used to fit the model, and ideally this should never be done. This limitation is relevant to our ability to predict across seasons using species-environment models. The datasets used for model building must include environmental data with values similar to those of the specified prediction period. Off California, where variables such as SST vary interannually as much as seasonally, it is possible to build multi-year summer models that include the range of environmental conditions in winter.

Seasonal predictive ability

Individual models for common dolphin, northern right whale dolphin, and Dall’s porpoise provided increased ability to predict distribution patterns across seasons, while estimates based on a null model (observations from the summer

shipboard surveys) were better than the GAM and GLM predictions for Risso's dolphin and Pacific white-sided dolphin. Most of the models exhibiting seasonal predictive ability showed good model fit (Becker et al. 2007, Chapter 3), emphasizing the importance of testing the explanatory power of a model prior to using it to make predictions on a novel dataset. These results were fairly consistent with results from a related study in which the same models were used to predict species density in summer/fall for the total shipboard study area (Becker et al. 2007, Chapter 3); the ratio of predicted/observed density estimates in that study for both model types was 0.900-0.998 for short-beaked common dolphin, 1.003-1.005 for Dall's porpoise, 0.819-0.830 for northern right whale dolphin, 1.345 for Risso's dolphin, and 0.665-0.674 for Pacific white-sided dolphin. Species for which the ratio of predicted/observed densities approached one in that study are the same that exhibited between-season predictive capabilities in this study (i.e., short-beaked common dolphin, northern right whale dolphin, and Dall's porpoise). Not surprisingly, the species models whose predictions were greater than 34% different from observed estimates (Pacific white-sided dolphin and Risso's dolphin) did not exhibit seasonal predictive capability as indicated by our rank analysis.

A notable difference between our results and those of Becker et al. (2007, Chapter 3) was evident in the "ship model predicting ship data" ranked density estimates for Dall's porpoise (Table 4.5). All Dall's porpoise models yielded similar density estimates for the total study area (all predictions were within 1% of density estimates derived from the observed shipboard data), indicating that the models are

robust when predicting over the large spatial scale of the entire survey region (Becker et al. 2007, Chapter 3). However, when predictions were made for the geographically stratified regions in this study, estimates were poor, as indicated by the relatively low rank correlation coefficients (less than 0.43; Table 4.5). Model results are often dependent on the scale at which data are collected and analyzed (Wiens 1989), and applying a model fitted with data from the entire study area to smaller spatial regions inherently includes the assumption that the factors determining density at small scales are the same as those at large scales (Gomez de Segura 2007). The poor performance evident at smaller spatial scales also could be attributed to the range of environmental variability present within the subregions in comparison to the entire study area. The models may have been able to capture distribution patterns over the study area given the wider range of variability, but were not able to capture finer-scale distribution patterns that have a more limited range of variability. These observations highlight the challenge often faced by marine resource managers who require cetacean distribution information for small-scale regions in order to evaluate the impacts of activities that are potentially harmful to cetaceans (e.g., Navy test and training activities); surveys often are conducted at larger spatial resolutions and predictions for these study areas may not be appropriate for smaller geographic scales.

Because results varied by species, the models' ability to predict seasonal distribution patterns and capture known species-environment relationships are discussed separately for each species below.

Short-beaked common dolphin. Short-beaked and long-beaked common dolphins cannot be reliably distinguished during aerial surveys, so the predictions made from the shipboard models built with short-beaked common dolphin sightings were evaluated based on aerial survey sightings that may have included both species; however, given the nearshore range of long-beaked common dolphins (Heyning and Perrin 1994), most of the *Delphinus* spp. sightings likely were short-beaked common dolphins. Predicted/observed density ratios for the total study area were fairly consistent for four different types of models, including the remotely sensed GAM and GLM considered in this study (Becker et al. 2007, Chapter 3), indicating model robustness. When these models were used to predict relative winter densities for the six geographically stratified areas, however, the GAM and GLM produced very different results (Table 4.5). This lack of robustness (results vary by model) at smaller spatial scales has been detected in other studies (Hedley and Buckland 2004; Ferguson et al. 2006). It is not clear why the GLM showed superior performance as compared to the GAM, because both the encounter rate and group size models included identical terms, and the functional forms were similar (Appendix A).

Significant seasonal differences in distribution have been documented for common dolphins, based on a statistical comparison of numbers of animals north and south of Point Arguello, and inshore/offshore of the 2,000 m isobath (Forney and Barlow 1998). The rank correlation test results suggest that the common dolphin GLMs were able to capture the variability in seasonal distribution. A visual comparison of the GAM and GLM density predictions indicates that both models

were able to identify the inshore/southerly shift in distribution observed during winter 1991-92, although the GLM was more effective at capturing the pattern, as indicated by the relatively higher densities and greater extent predicted for the Southern California Bight (SCB; Figure 4.5a). Both the GAM and GLM predictions were notably different than those for summer, where short-beaked common dolphins were predicted to occur well north of Point Arguello (Becker et al. 2007, Chapter 3).

Risso's dolphin. The failure of the models to accurately predict seasonal distribution patterns of Risso's dolphin suggests that the environmental variables used in this study are not effective at capturing distribution patterns for this species, as also noted in Becker et al. (2007, Chapter 3). Other studies have found Risso's dolphin to be associated with the continental slope and in regions with steep bathymetry (Dohl et al. 1978, 1983; Green et al. 1992; Baumgartner 1997, 2001); however, neither the slope nor zone variables were included in the final models for this species. Risso's dolphin sightings were most numerous in the SCB during both the summer ship surveys and winter aerial surveys, and animals also were observed off central California during both surveys. A comparison of the abundance and distribution patterns of this species between the two periods indicated a significant increase in abundance during winter, but no significant difference in distribution within the study area (Forney and Barlow 1998). However, during the summer ship surveys, Risso's dolphins were also sighted in offshore waters of northern California, west of the aerial survey study area. This species occurrence in habitats with very different oceanographic characteristics (i.e., waters of the SCB, California Current,

and offshore subtropical gyre) presents challenges to modeling habitat using broad environmental descriptors such as SST, as the models are not able to effectively differentiate among water masses.

The relative distribution patterns produced by the GAM and GLM suggest that both models over-predicted densities north of Monterey Bay, where waters in the study area tend to be cooler (Figure 4.5b). This is most likely due to the linear SST function in the group size models, which showed increasing group sizes with decreasing water temperatures (Appendix A). The 1991-2001 shipboard survey data upon which the models were built included only one sighting of Risso's' dolphin in waters cooler than 14.5° C (in 1996 there was one sighting of 150 animals in 12° C waters). This sighting was probably partially responsible for the models' linear SST function, which in turn contributed to the predicted high densities in cool waters that were more prevalent in winter. In order to get more reliable models for this species, additional survey data are needed in relatively cool waters, such as those experienced during a La Niña event. Extending the analysis to include more northerly geographical areas might also be helpful in this regard.

Pacific white-sided dolphin. The modeled densities by stratum for the Pacific white-sided dolphin compared well to the shipboard summer data used to build the models, indicating good regional explanatory power. The Spearman rank correlation coefficients were significant for encounter rate ($r = 0.957$), group size ($r = 0.900$), and density ($r = 0.900$), indicating that the predicted ranks matched very well with those estimated from the observed data. The models failed to effectively

predict winter densities, however, as indicated by the rank correlation tests (Table 4.5). The lack of between-season predictive ability could be due in part to the small sample sizes available for both building the models and evaluating their predictive performance: 25 sightings from the summer shipboard surveys were used to build the models and only 15 sightings were available from the winter aerial surveys for the rank correlation analysis. Visual inspection of the density plots for this species suggest that the models' predictive ability was better than indicated by the rank correlation test, as relatively higher densities were predicted in the areas where Pacific white-sided dolphins were sighted during the 1991-92 aerial surveys (Figure 4.5c). These plots also show that highest densities were predicted for cool waters north of Cape Mendocino. These are likely over-predictions due to the somewhat linear functions for SST in waters less than about 12° C, which were included in the encounter rate models for this species (Appendix A).

The predictive ability of cetacean-environment models built with remotely sensed data may vary by habitat, because cloud cover is more prevalent in cool-water regions off California, reducing the number of satellite data available. In addition, cetacean-environment models are affected by the level of complexity of the oceanographic environment, because more data are required to parameterize models for species that inhabit diverse environments (Becker et al. 2007, Chapter 3). Both of these factors affect models built for the Pacific white-sided dolphin, as this species occurs primarily in shelf and continental slope waters off California that are prone to coastal fog/cloud cover, and it inhabits complex oceanographic

environments (e.g., highly variable bathymetry, water temperature, etc.). Ironically, more data are required to build models for this species but satellite data are more limited by cloud cover. To increase the predictive ability of the Pacific white-sided dolphin models built with remotely sensed data, additional surveys in clear conditions are required. Additional alternatives to help prevent data loss due to cloud cover include the collection of remote sensing data from the survey aircraft and the use of microwave radiometers.

Northern right whale dolphin. The GAMs for northern right whale dolphin exhibited consistently good predictive performance as indicated by the rank correlation tests (Table 4.5). Despite the GLM's unrealistic predictions for encounter rate (see "Performance of GAMs vs. GLMs" above), when evaluated based on relative density by stratum, the GLM predictions were better than those of the null model. Forney and Barlow (1998) identified a statistically significant difference in the abundance of northern right whale dolphin between the summer and winter survey periods assessed in this study, with more animals present during the cold water period. In addition, they found a significant difference in distribution of this species within the study area, and provided additional evidence for an influx of animals into the SCB in winter as noted previously by Leatherwood and Walker (1979) and Dohl et al. (1978). Based on the results of the rank correlation tests, the models were able to effectively capture the relative distribution pattern of seasonal variability. However, the extreme over-predictions in northern waters are shown clearly in the GLM, and to a lesser extent, the GAM density plots (Figure 4.5d).

Similar to the models for Risso's dolphin and Pacific white-sided dolphin, the SST functions in the encounter rate models for northern right whale dolphin produced unreliable estimates in waters cooler than those included in the summer shipboard survey data. In addition, although the models predicted moderately low levels of relative density within the SCB, they clearly did not capture the full extent of the pattern, as indicated by the concentration of sightings in the continental shelf and slope regions of the SCB during the 1991-92 aerial surveys. In summary, while the models exhibited some predictive ability, more data collected over a range of oceanographic conditions are needed to make the models robust and allow them to capture seasonal patterns throughout the study area.

Dall's porpoise. The encounter rate models for Dall's porpoise exhibited the greatest difference in predictive power between GAM and GLM, and this was one of only two species for which the predictor variables included in the final models differed by more than one term (Table 4.3). The GAM was more complex (additional terms and degrees of freedom), and included two variables that did not show up in the final GLM: CV(SST) and the categorical oceanographic zone variable. The effect of CV(SST) on the mean response was minimal, while zone showed an effect opposite to that indicated by the depth function. In this case, due to the high correlation between the depth and zone predictor variables, zone was included as noise in the GAM (Appendix A). In some cases a second variable that indicates an opposite trend can be meaningful; however, zone was the last term to enter the model and it explained very little deviance (Becker et al. 2007, Chapter 3).

Dall's porpoise are found in shelf, slope, and offshore waters (Morejohn 1979), but the majority (62%) of sightings during the 1991-92 aerial surveys were in waters with depths less than 2,000 m. Functional forms for slope, SST, and Beaufort were similar in the two types of models. However, the depth function was more linear in the GAM than in the GLM, predicting more encounters in shallow waters, consistent with encounter rate GAMs built with a subset of these data (Forney 2000). The polynomial in the GLM had a broad maximum between approximately 1,900 and 2,222 m, with encounters decreasing on either side, indicating that the GLM most likely overestimated encounters in deeper waters, and underestimated encounters in waters shallower than 1,900 m.

Previous analyses of a portion of the cetacean sighting data used for this study (the 1991 shipboard survey data and the 1991-1992 aerial survey data) found a statistically significant seasonal difference in the distribution of Dall's porpoise north and south of Point Arguello, documenting a southward shift during winter (Forney and Barlow 1998). The GAMs were able to effectively capture this seasonal change in distribution, as indicated by the rank correlation test (Table 4.5). Visual inspection of the density plots for this species suggests that the GLM actually was more effective at predicting an influx of animals south of Point Arguello during winter (Figure 4.5e). A comparison of the GAM's density predictions for winter (Figure 4.5e) to the same model's density plot for summer (see Appendix B.f) provides clear evidence that the summer shipboard models effectively predicted winter distribution patterns for Dall's porpoise; in summer, densities are highest

north of San Francisco, with few animals present in the SCB, while the winter predictions captured this species southerly shift in distribution as noted above.

Caveats

In many regions with clearly distinctive seasonal differences (e.g., polar regions), it would not be appropriate to use models built with summer data in an attempt to make winter predictions. Off California, however, where interannual variability can mimic seasonal variability, it is possible for some species to build multi-year summer models that include the range of environmental conditions occurring in winter. To be effective, the datasets used for model building must include environmental data with a range of values that overlap those of the specified prediction period. As demonstrated here, significant errors can result when relying on model predictions that have been extrapolated beyond the range of values used to fit the model. This is a critical issue for predicting across seasons using species-environment models. When the range of environmental variables from the two seasons overlapped, the models were able to capture the shifts in seasonal distribution patterns for three of the five species considered in this study.

Across-season predictions are not appropriate for highly migratory species that are known to be absent from the study area in either the season used for model building or the season for which predictions are made, e.g., many baleen whales. The environmental variables used for modeling will not reflect the absence of species that move to different areas for seasonal breeding. Social organization and

behavioral aspects of species ecology may also confound the cetacean-habitat modeling approach, particularly when attempting to predict across seasons.

While autocorrelation is expected to be present in the sighting and environmental data used for this analysis, we did not examine it. A primary goal of this study was to produce models that could be used to predict seasonal distribution patterns of cetaceans based on a set of environmental variables. Predictive models are distinct from similar models used to test hypotheses, where the potential bias in variance estimates due to autocorrelation and inflated sample size can lead to incorrect conclusions regarding underlying mechanisms. Autocorrelation does not severely bias the parameter estimates for the smooth functions (Neter et al. 1990), nor is the absence of autocorrelation a requirement for effective predictive modeling (Hamazaki 2004). Nonetheless, the presence of autocorrelation in model residuals can affect variance estimation associated with the predictions. Our predictive analysis was based on a comparison of ranked (not actual) density estimates, so we did not estimate variance in the predictions. There are numerous sources of uncertainty associated with GAM predictions (Ferguson et al. 2006), and variance estimation is the subject of ongoing research.

The pseudo-jackknife cross validation process used to select the final encounter rate and group size models was optimized for the summer survey data. Future modeling efforts aimed at predicting densities across seasons should consider allowing additional variables into the final models. For example, variables that were included in some of the (n-1)-year models but did not make it into the final model

could be allowed in the list of predictors. Their ability to predict across seasons might be better than suggested from the cross validation process based solely on summer data.

The number of sightings available for our seasonal analysis was low, and there were inherent limitations in a rank correlation test that analyzed only six pairs of data. The number of sighting data available for building the models has a large effect on their resulting predictive ability (Becker et al. 2007, Chapter 3), as does the number of sightings available to assess model performance. For example, 21 Pacific white-sided dolphin groups were sighted during the 1991-1992 aerial surveys, and only 15 of these had corresponding satellite-derived SST data. When the 15 sightings were stratified for the geographic analysis, one stratum contained only one sighting of 77 animals, which had a large effect on the group size rankings.

Future studies should investigate the predictive power of SST averaged over greater spatial and temporal resolutions (Becker et al. 2007, Chapter 3). In addition, SST data obtained from newer microwave radiometers will help prevent data loss due to cloud cover and should be evaluated in future studies.

We evaluated seasonal predictive ability based on correlations between the models' predicted density ranks and those calculated from the aerial survey data, inherently including the assumption that the observed data are the "truth." There are many sources of error associated with collecting and analyzing line-transect data (Ferguson et al. 2006), including measurement error associated with the number and location of sightings. Theoretically, the models could correctly predict a higher

density in one of the strata, but by chance no animals were observed during the aerial surveys.

Conclusions

Results of a simple rank correlation test suggest that, when predicting across seasons, geographic patterns of species density were captured to some extent for at least three of the five species considered. The models that exhibited seasonal predictive capability were for species known to have significantly different patterns of seasonal distribution in the study area. These results suggest that, although the processes of interannual and seasonal variability are different, interannual variability in the environmental parameters can be large enough to explain some of the variation in the seasonal distribution patterns of cetaceans in the waters off California. The poor seasonal predictive performance evident for some of the models could be due in part to the small number of sightings available for building the models. More importantly, models need to be developed using environmental parameters that include the full range of conditions for the temporal/spatial period they are predicting. Future modeling efforts, particularly those that include remotely sensed environmental variables, require additional data to refine and improve the predictive ability of species-environment models. For the California study area specifically, additional survey data collected during the winter or during strong La Niña episodes are needed to capture seasonal distribution patterns and produce more realistic density estimates for cool water conditions. For some species, this might also be

achieved by expanding the study area to include a broader range of environmental conditions.

Ideally, cetacean survey data would be collected for the specific time period of interest and cetacean-habitat models built accordingly. However, poor weather conditions and high sea states off California during winter prohibit the completion of comprehensive shipboard surveys. Although aerial surveys have been used to collect data during the winter, there are drawbacks associated with both the collection and analysis of these data. First, safety issues and fuel capacity usually prevent surveys of large areas offshore and limit the size of the study area that can be covered. In addition, availability bias is much greater for aerial surveys as compared to ship surveys, and correction factors to account for this bias have been developed for only a few species. Therefore, more aerial survey data are required in order to obtain a sufficient number of sightings for most species. Ship surveys more readily provide the sample sizes required for modeling, and if additional summer surveys could capture the full range of seasonal environmental variability, results from this study suggest that variation in the seasonal distribution patterns of some cetacean species off California could be predicted. In lieu of actual winter survey data from recent years, winter densities currently are estimated from summer shipboard surveys without consideration of environmental data (i.e., our “null” model). Assuming adequate summer data are available, across-season predictions from cetacean-habitat models will represent an improvement to the null model for some species.

A comparison of within-season (summer/fall) density predictions made for the total shipboard study area of approximately 818,000 km² to relative density predictions for six geographically stratified areas within the aerial study region (approximately 264,000 km²) reveals apparent differences in the predictive ability of models at different spatial scales. Care should be taken when estimating cetacean abundance for spatial resolutions that are smaller than the resolutions at which the models were built. Overall results of the rank correlation tests indicate that GAMs had better between-season predictive ability than GLMs, due in part to unrealistic values predicted by polynomials when applied to data outside of the range used to build the models. Ideally, predictions should not be made outside of the variable range used for model development.

For some species, such as Risso's dolphin, simple oceanographic measures like SST do not appear to capture the species-environment relationships sufficiently to predict species densities. Ongoing analyses to develop prey indices may improve predictive models, but their use requires intensive sampling and data processing, and they have limited use in generating predictions for novel time periods or in near real-time. Remotely-sensed environmental predictor variables are available in near real-time at a range of spatial and temporal scales, and are critical for models that must rely on aerial survey data (sensors can be placed on survey aircraft but measurements would not be as synoptic as those provided by satellite data). Risso's dolphins occur in habitats with very different oceanographic characteristics (i.e., waters of the SCB, California Current, and offshore North Pacific gyre), and if proxy measures for

different water masses could be developed based on remotely sensed variables, our predictive modeling capability would likely improve. Latitude and longitude interaction terms have been used in predictive models to capture differences in location of water masses with similar properties (Forney 2000); however, a water mass proxy variable would eliminate the need to include fixed geographic points in habitat models and thus enhance their use for prediction in dynamic environments. Future analyses should focus on increasing our ecological understanding of cetacean prey distributions, and using this knowledge to develop more effective proxy measures from satellite-derived data.

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Table 4.1. Summary of satellite-derived sea surface temperature (SST) and CV(SST) spatial resolutions with the greatest predictive ability for encounter rate and group size GAMs and GLMs (from Becker et al. 2007, Chapter 3). Numbers refer to the number of pixels included in the resolution. The spatial resolutions tested included 1, 4, 9, 16, 25, and 36 pixel boxes, corresponding to 5.55-33.3 km boxes (i.e., 30.8 – 1,108.9 km²).

Species	Encounter Rate		Group Size	
	SST	CV(SST)	SST	CV(SST)
Short-beaked common dolphin	36	36	36	25
Risso's dolphin	9	16	36	16
Pacific white-sided dolphin	36	9	36	9
Northern right whale dolphin	36	9	36	36
Dall's porpoise	25	36	36	36

Table 4.2. Total number of segments and sightings used to build the predictive models based on data from the 1991, 1993, 1996, and 2001 shipboard surveys of California waters in summer/fall ("shipboard"), and the number of segments and sightings used to evaluate the models based on data from the 1991 and 1992 aerial surveys of California waters in winter/spring ("aerial"). The numbers are based on segments for which remotely sensed SST data were available for species-specific resolutions (see Table 4.1 above) and reflect sightings in Beaufort sea states 0-5 that were used in this analysis.

Species	Survey			
	shipboard		aerial	
	segments	sightings	segments	sightings
Short-beaked common dolphin	6,054	316	2,533	31
Risso's dolphin	6,054	70	2,533	14
Pacific white-sided dolphin	5,500	25	2,324	15
Northern right whale dolphin	6,030	40	2,533	23
Dall's porpoise	5,928	179	2,480	37

Table 4.3. Comparison of the variables included in the final encounter rate and group size GAMs and GLMs built with remotely sensed SST and CV(SST). Linear fits are represented by “L1”. Smoothing splines (GAMs) are represented by “S#” and polynomial (GLMs) are represented by “P#”, where # is the associated degrees of freedom. Note that zone is a categorical variable. For those species where the GAM and GLM included different predictor variables and/or degrees of freedom, the variable codes are shown in bold.

Encounter Rate Models		Predictor Variables					
Species		Zone	Depth	Slope	SST	CV(SST)	Beaufort
Common dolphin	GAM	L1			S3		L1
	GLM	L1			P3		L1
Risso's dolphin	GAM		L1				
	GLM		L1				
Pacific white-sided dolphin	GAM	L1	S3		S3	S3	
	GLM	L1	P2	L1	P3	L1	
Northern right whale dolphin	GAM	L1			S3		S3
	GLM	L1			P3		P3
Dall's porpoise	GAM	L1	S3	S3	S3	S2	S3
	GLM		P2	P3	P2		L1

Group Size Models		Predictor Variables					
Species		Zone	Depth	Slope	SST	CV(SST)	Beaufort
Common dolphin	GAM				L1		L1
	GLM				L1		L1
Risso's dolphin	GAM				L1		
	GLM				L1		
Pacific white-sided dolphin	GAM						L1
	GLM						L1
Northern right whale dolphin	GAM				L1	L1	
	GLM				L1	L1	P2
Dall's porpoise	GAM			L1			L1
	GLM			L1			L1

Table 4.4. Summary of the weighted effective strip width ($ESW = 1/f(0)$) estimates used to calculate observed and predicted densities for this analysis. The original values are those estimated from all the survey data (Forney and Barlow 1998, Barlow 2003). The weighted values were based on the proportion of groups within each group size range observed during the combined surveys within each geographic stratum or combined geographic stratum resulting from the K-S tests. Survey: (A) 1991-2001 ship surveys, and (B) 1991-1992 aerial surveys.

(A.) SHIP SURVEY

Species	Group size	Original ESW	Weighted ESW by Strata					
			1A	1B	1C	2A	2B	2C
Short-beaked common dolphin	1-20	0.50						
	21-100	1.24	1.48	1.48	1.24	1.48	1.48	1.24
	100+	1.84						
Risso's dolphin	1-20	1.37						
	20+	2.18	1.68	1.68	1.68	1.68	1.68	1.68
Pacific white-sided dolphin	1-20	0.50						
	21-100	1.24	0.71	0.71	1.16	0.71	0.71	1.16
	100+	1.84						
Northern right whale dolphin	1-20	0.50						
	21-100	1.24	0.59	0.59	0.59	0.59	0.59	0.59
	100+	1.84						
Dall's porpoise ¹	all	0.82	0.82	0.82	0.82	0.82	0.82	0.82

(B.) AERIAL SURVEY

Species	Group size	Original ESW	Weighted ESW by Strata					
			1A	1B	1C	2A	2B	2C
Short-beaked common dolphin	1-10	0.21						
	10+	0.35	0.32	0.32	0.32	0.32	0.32	0.32
Risso's dolphin	1-10	0.21						
	10+	0.35	0.29	0.29	0.29	0.29	0.29	0.29
Pacific white-sided dolphin	1-10	0.50						
	10+	1.24	1.05	1.05	1.05	1.05	1.05	1.05
Northern right whale dolphin	1-10	0.50						
	10+	1.24	0.67	0.67	0.67	0.67	0.67	0.67
Dall's porpoise ¹	all	0.21	0.21	0.21	0.21	0.21	0.21	0.21

¹For Dall's porpoise, the original estimates were applied to effort in Beaufort sea states 0-2. For this analysis they were applied to effort in Beaufort sea states 0-5 to maintain the maximum possible sample size for modeling. This resulted in a downward bias in our density estimates.

Table 4.5. Summary of Spearman rank correlation coefficients. The "Ship GAM" and "Ship GLM" are the models built with the summer/fall shipboard data. The "Ship (NULL)" are the values estimated from the summer/fall shipboard surveys using standard line-transect methods in the absence of environmental data. The "Ship Obs" and "Air Obs" data are the summer/fall shipboard observed and winter/spring aerial observed values. For example, the "Ship GAM" and "Ship GLM" models predicting on the "Ship Obs" data reflect results obtained when the models were used to predict data from the shipboard surveys upon which they were built (essentially a measure of goodness of fit). The critical value at $\alpha = 0.05$ (one-tailed test) with five degrees of freedom is $r_{crit} = 0.829$ (i.e., values are significant if larger). Significant correlations are marked with an asterisk (*), and cases for which the predicted aerial values did better than the null model are shown in bold.

Correlations		Species				
Model	Data	Common dolphin	Risso's dolphin	Pacific white-sided dolphin	Northern right whale dolphin	Dall's porpoise
Encounter Rate:						
Ship GAM	Ship Obs	0.429	0.657	*0.957	*0.843	*0.829
Ship GLM	Ship Obs	0.486	0.657	*0.957	*0.957	0.771
Ship (NULL)	Air Obs	0.214	0.014	0.257	0.314	0.714
Ship GAM	Air Obs	0.129	-0.443	0.014	0.729	0.886
Ship GLM	Air Obs	0.500	-0.443	0.014	0.543	-0.200
Group size:						
Ship GAM	Ship Obs	*0.886	-0.029	*0.900	*0.957	0.086
Ship GLM	Ship Obs	*0.886	-0.029	*0.900	*0.957	0.029
Ship (NULL)	Air Obs	0.500	0.700	0.486	0.257	-0.371
Ship GAM	Air Obs	0.871	0.357	0.014	0.557	0.429
Ship GLM	Air Obs	0.729	0.357	0.129	0.714	0.086
Density:						
Ship GAM	Ship Obs	*0.829	0.086	*0.900	*0.843	0.429
Ship GLM	Ship Obs	*0.829	0.086	*0.900	*0.957	0.371
Ship (NULL)	Air Obs	0.214	0.129	0.257	0.371	0.200
Ship GAM	Air Obs	0.129	-0.414	0.014	0.786	0.543
Ship GLM	Air Obs	0.500	-0.414	0.129	0.486	-0.486

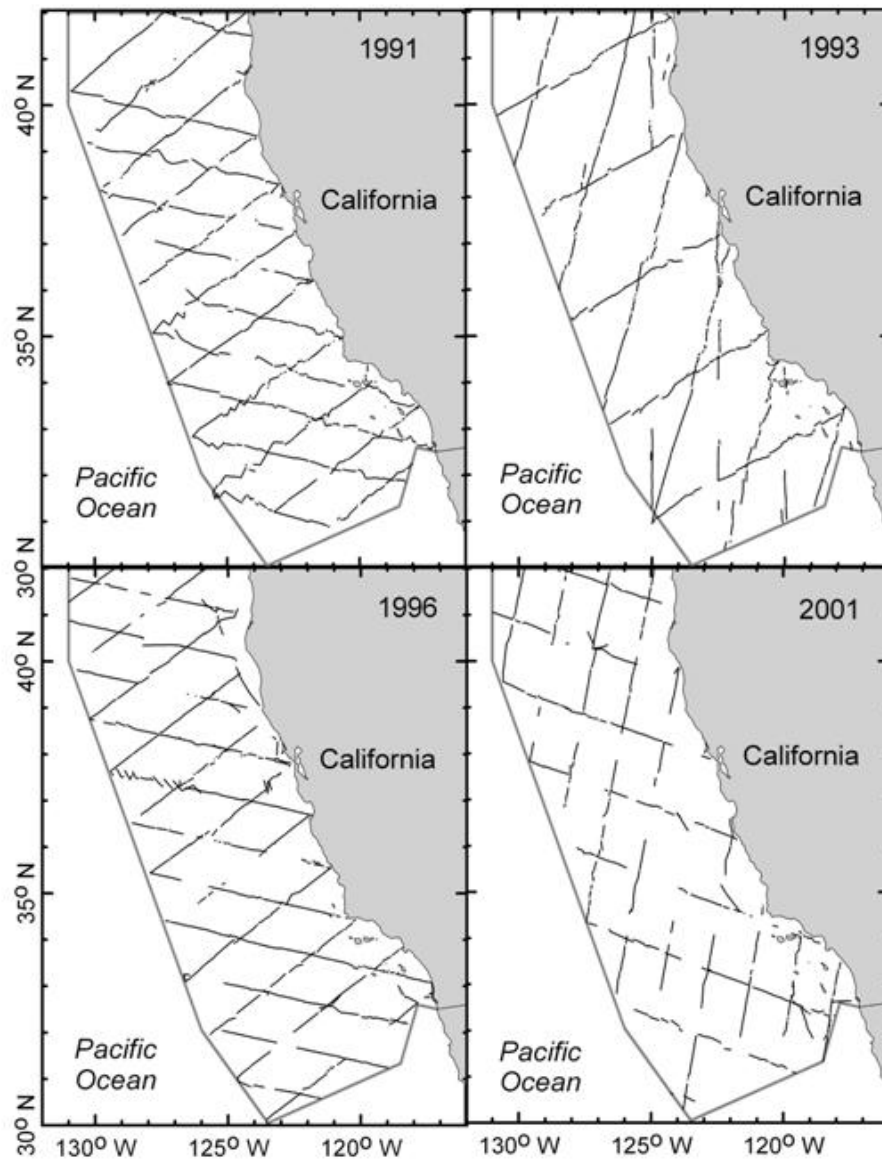


Figure 4.1. Completed transects for the shipboard line-transect surveys conducted late July through early December 1991, 1993, 1996, and 2001 off California in Beaufort sea states of 0-5. The study area encompasses approximately 818,000 km². One degree of latitude = 111 km.

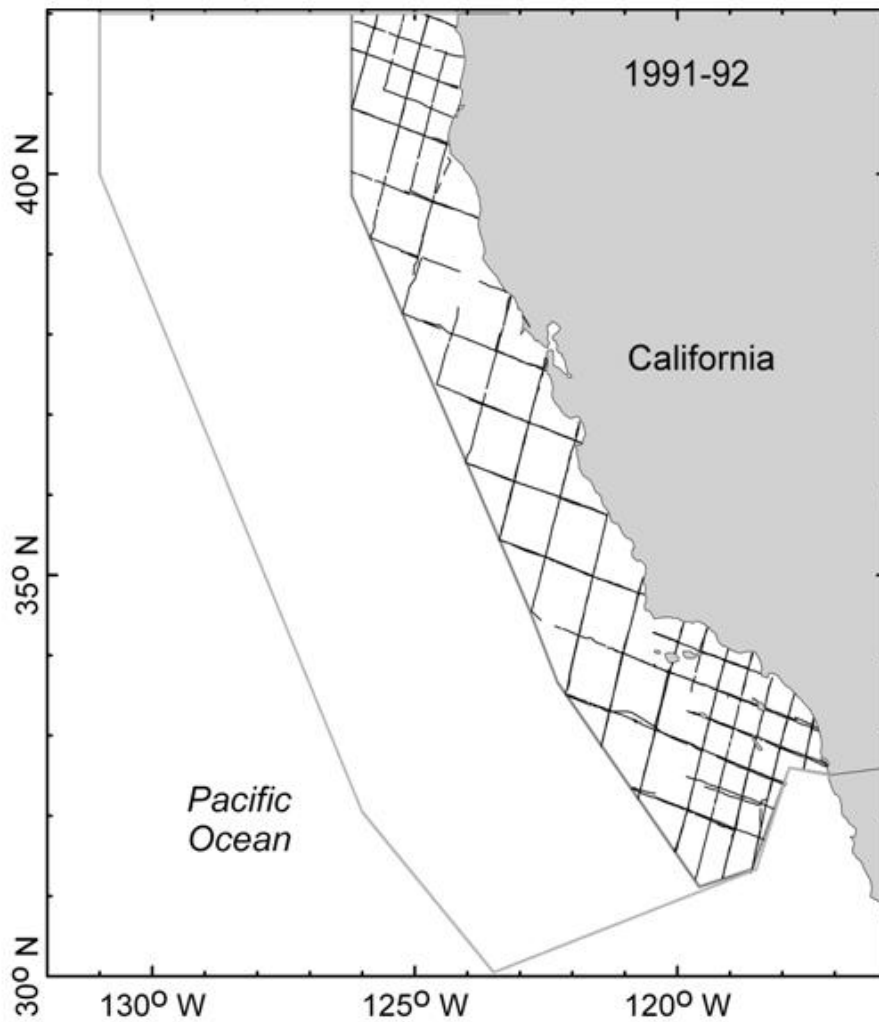


Figure 4.2. Completed transects for the aerial line-transect surveys conducted off California in March-April 1991 and February-April 1992 in Beaufort sea states of 0-5. The light gray line west and offshore of the aerial study area marks the full study area used to develop the summer models (i.e., the outer boundary of the shipboard line-transect study area). One degree of latitude = 111 km.

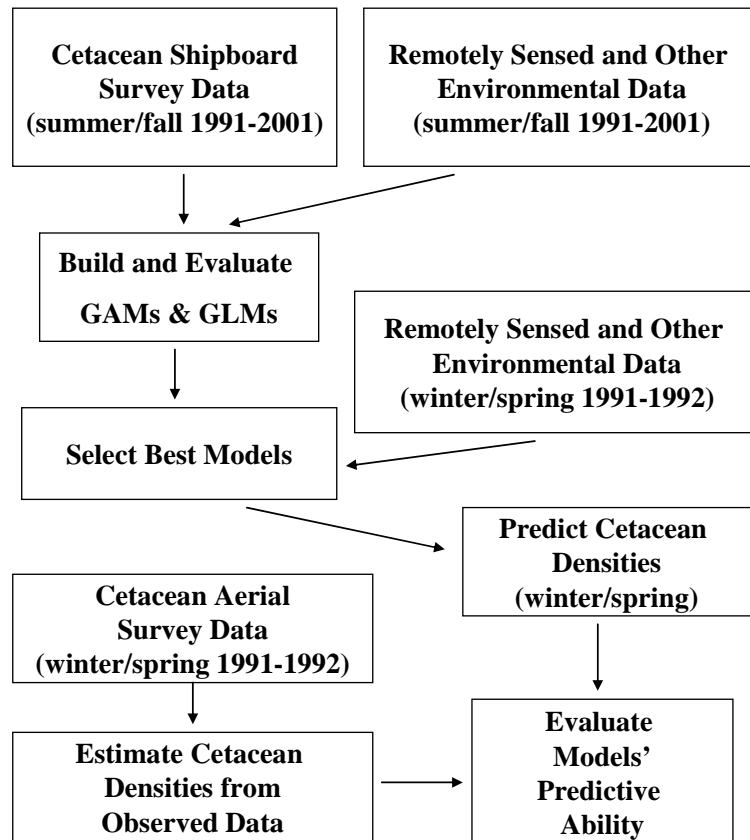


Figure 4.3. Steps for evaluating predictive ability across seasons.

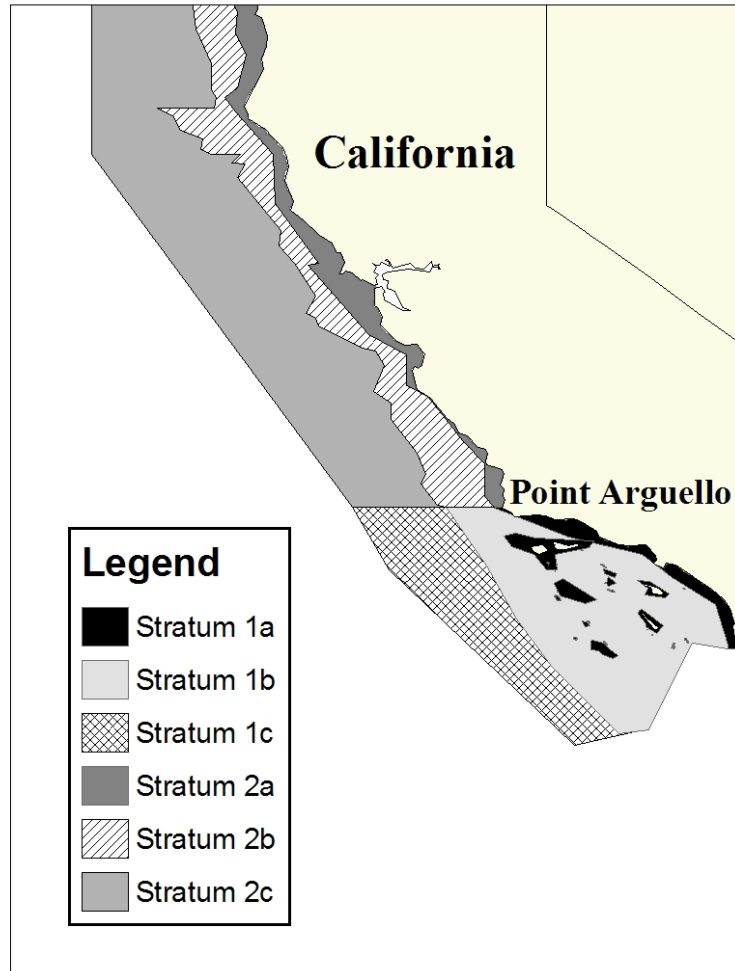
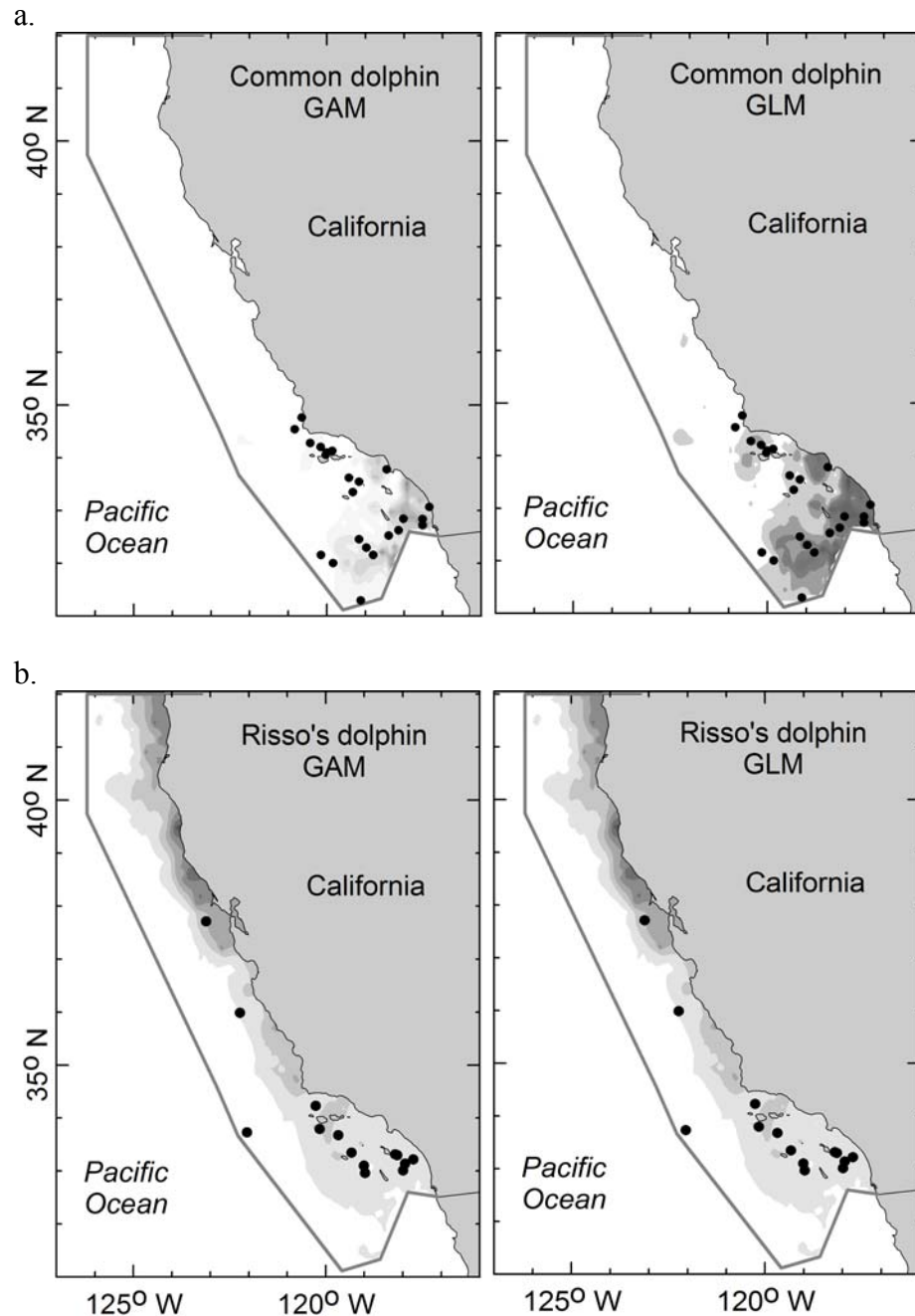
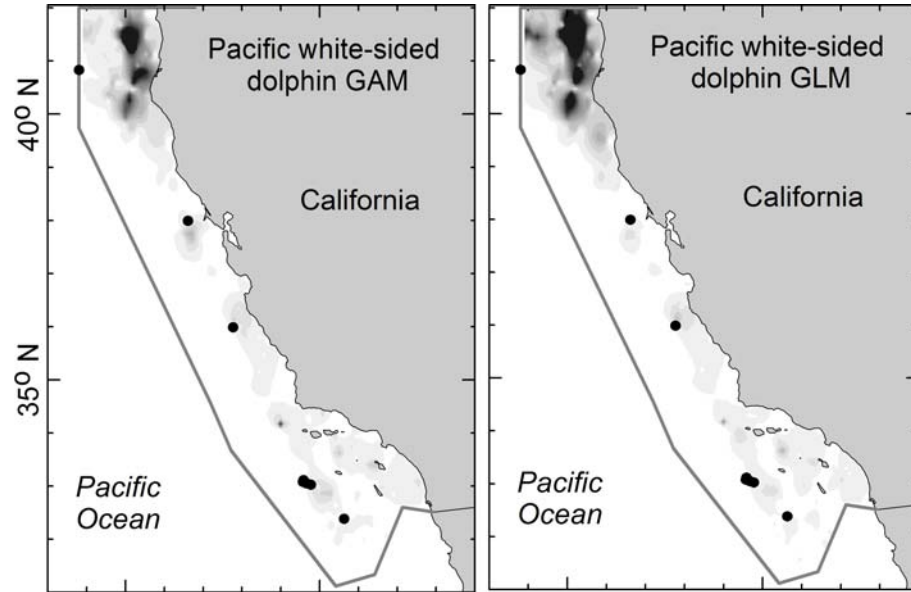


Figure 4.4. Geographic strata used for Spearman rank correlation tests.

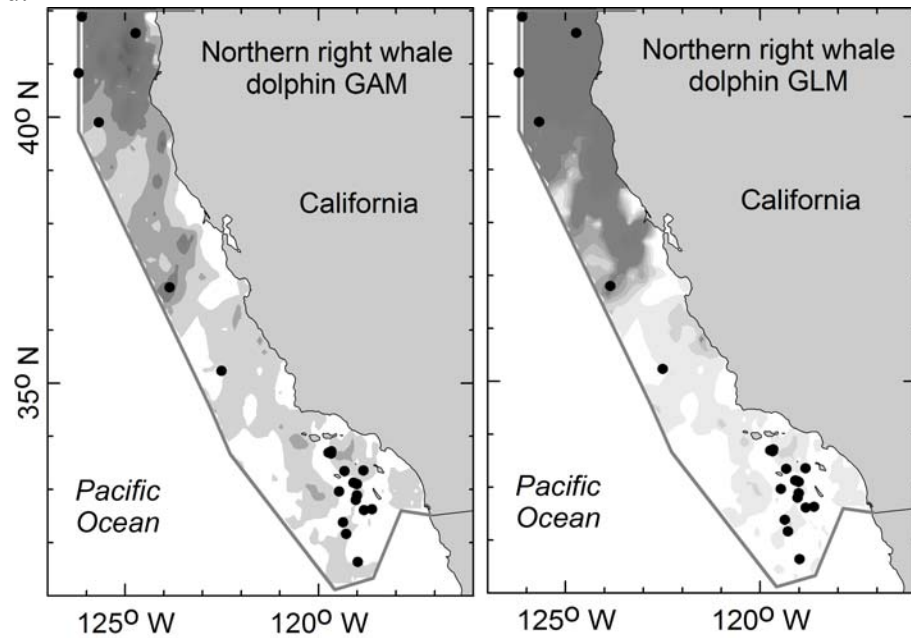
Figure 4.5. Predicted densities for winter/spring based on winter/spring environmental data and on summer/fall shipboard models, for (a) common dolphin, (b) Risso's dolphin, (c) Pacific white-sided dolphin, (d) northern right whale dolphin, and (d) Dall's porpoise. Predicted values were smoothed using inverse distance weighting (see Methods for more details). Colors indicate relative density (i.e., darker = higher). Black dots show winter/spring sighting locations.



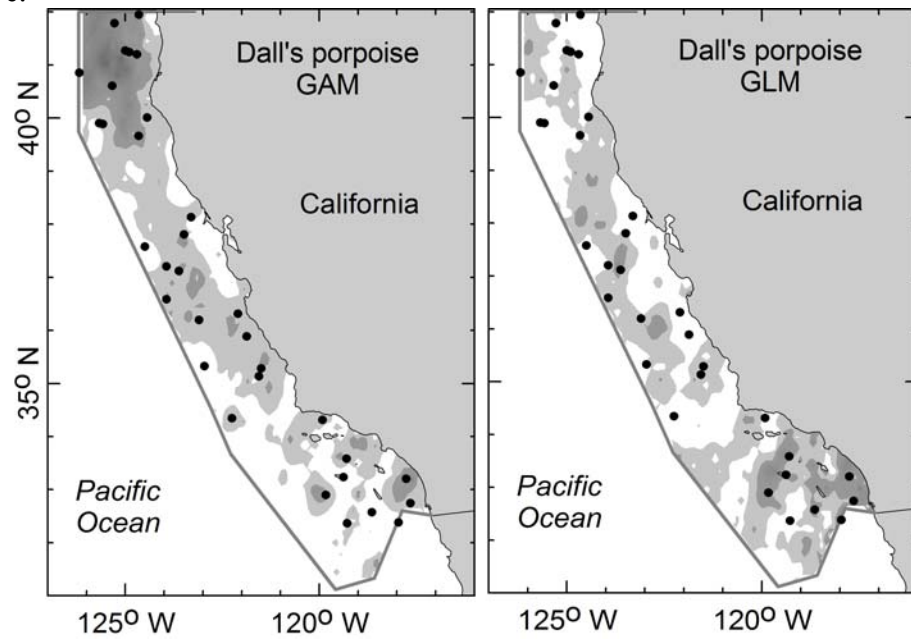
c.



d.



e.



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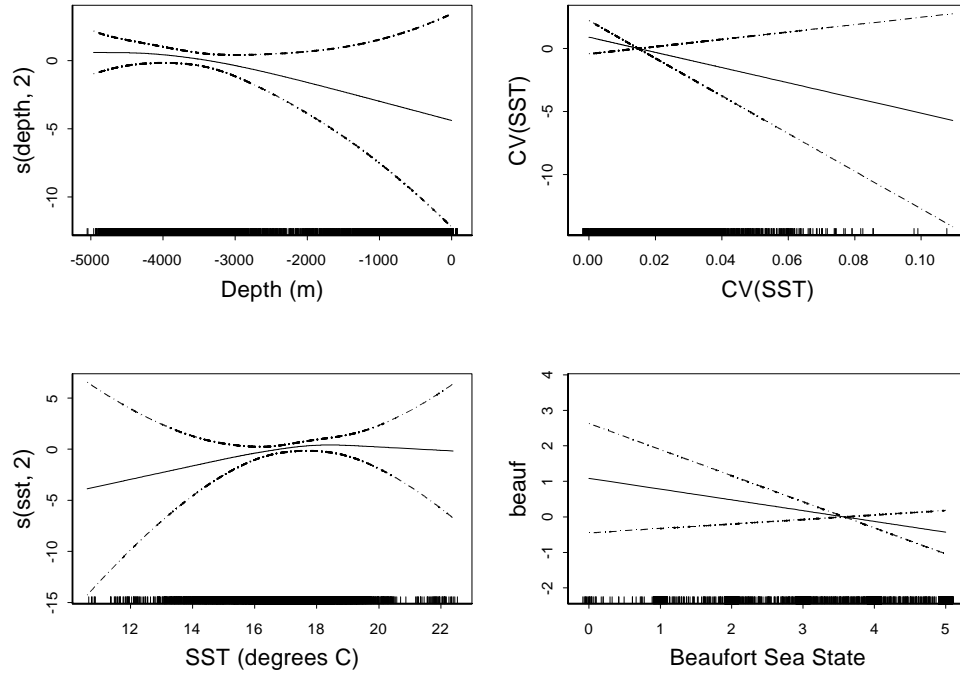
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Appendix A

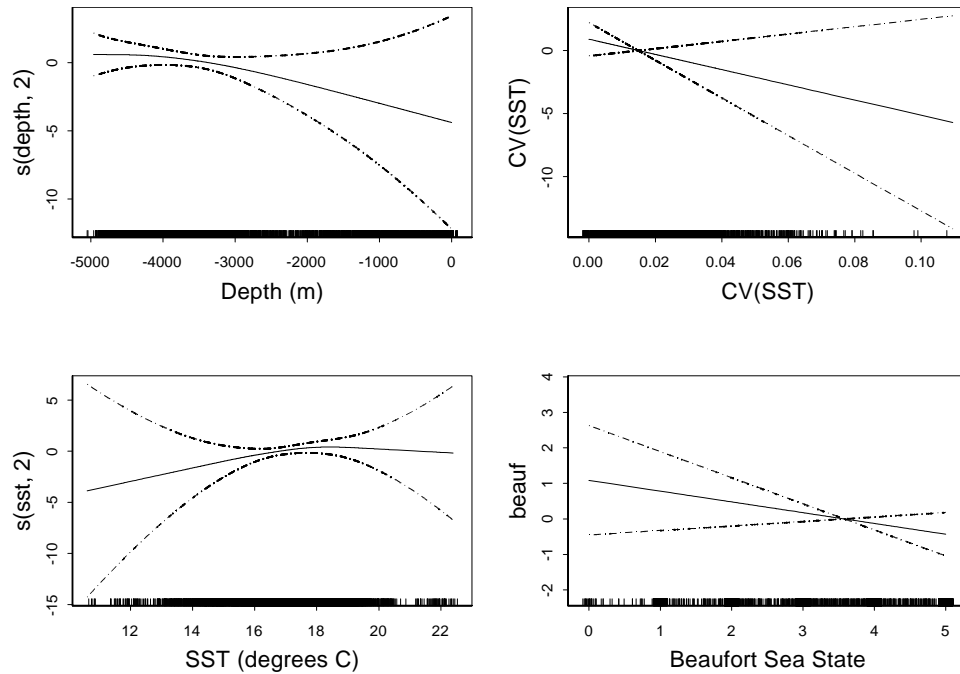
Shapes of the functional forms of the predictor variables included in the final encounter rate and group size generalized additive and generalized linear models for (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso's dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall's porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, and (j) humpback whale. Functions are shown for models built with remotely sensed (1) and *in situ* (2) sea surface temperature (SST) and coefficient of variation (CV) of SST data. Models were constructed with both linear terms and smoothing splines (s) for the generalized additive models (GAMs) or polynomials (poly) for the generalized linear models (GLMs) having up to three degrees of freedom. The y-axes represent the smoothing spline or polynomial function. Degrees of freedom for nonlinear fits are noted in the parentheses on the y-axis. Zero on the y-axes corresponds to no effect of the predictor variable on the estimated response variable (encounter rate or group size). Functions have been scaled relative to the variable having the largest y-axis range that was not influenced by outliers. Data points for each variable are indicated by the tick marks above the x axis. The dashed lines reflect 2x standard error bands (i.e., 95% confidence interval). Zone was modeled as a categorical variable defined roughly by water depth: 1 = shelf (waters from the coast to 200 m deep), 2 = slope (waters between 200 m and 2,000 m), and 3 = abyssal plain (waters deeper than 2,000 m).

(a.1) Striped dolphin

Encounter rate GAM built with remotely sensed data

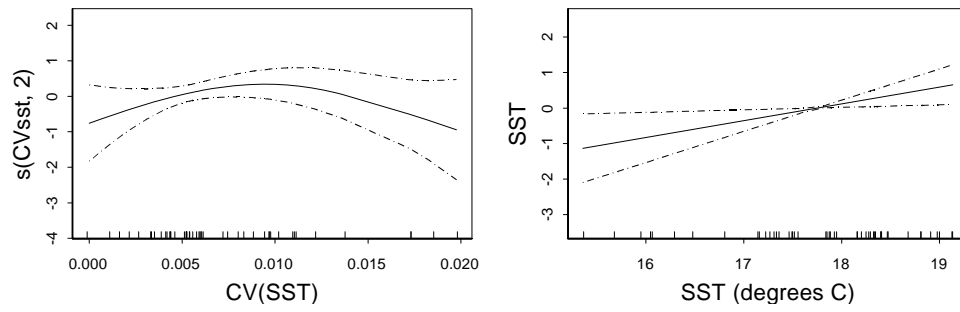


Encounter rate GLM built with remotely sensed data

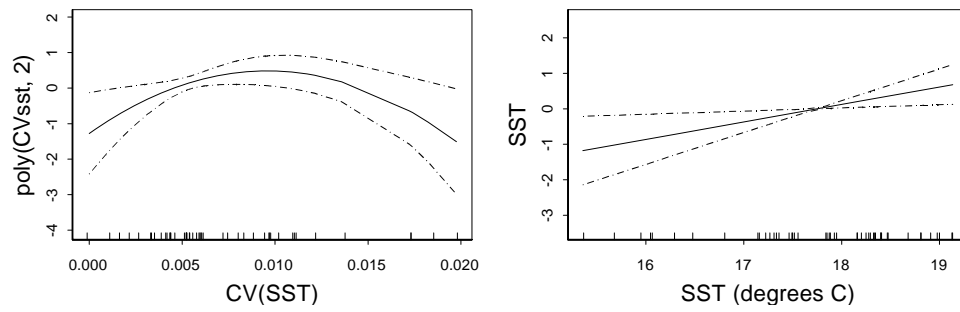


Striped dolphin (continued)

Group size GAM built with remotely sensed data

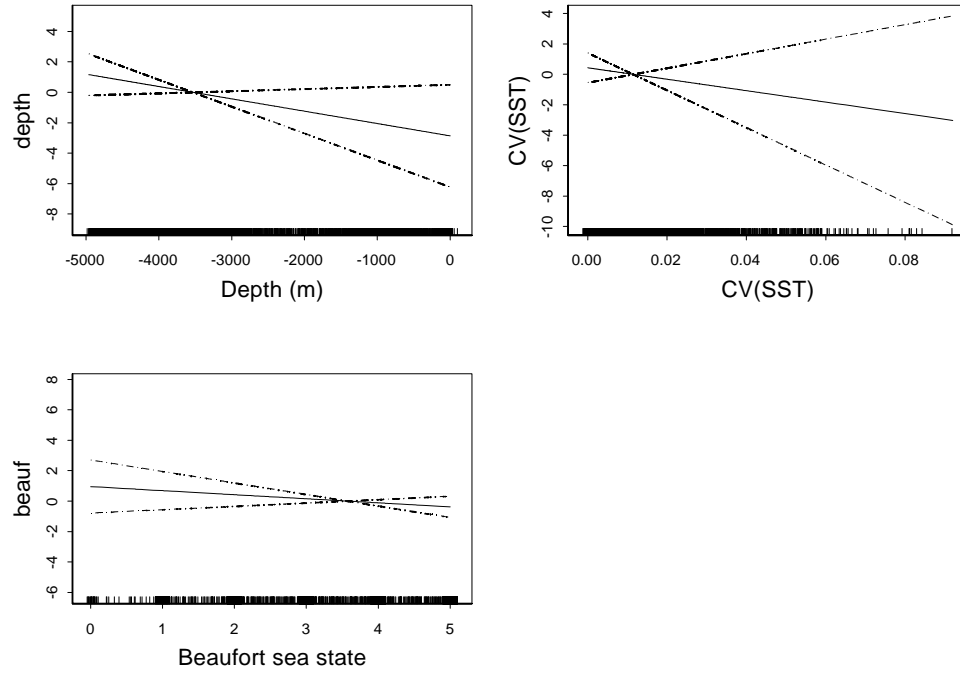


Group size GLM built with remotely sensed data

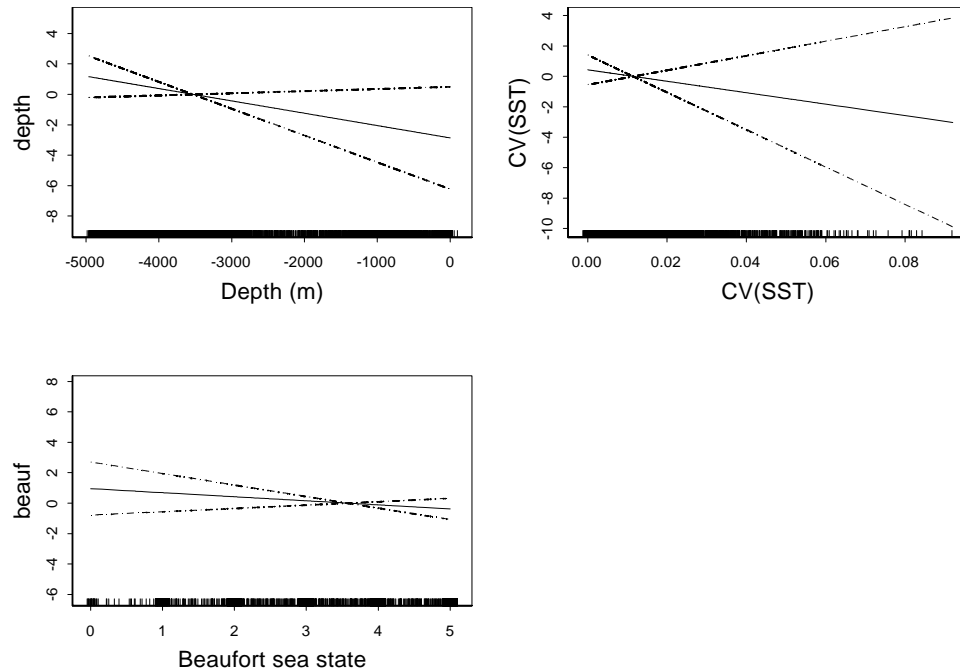


(a.2) Striped dolphin

Encounter rate GAM built with *in situ* data

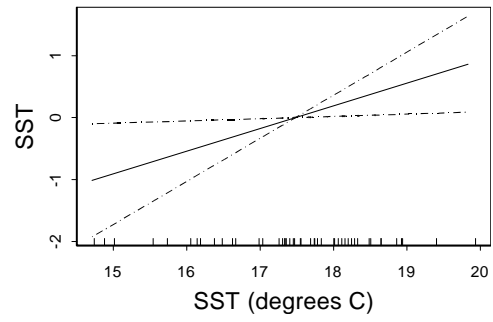


Encounter rate GLM built with *in situ* data

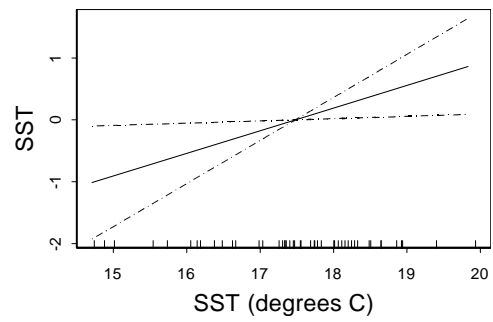


Striped dolphin (continued)

Group size GAM built with *in situ* data

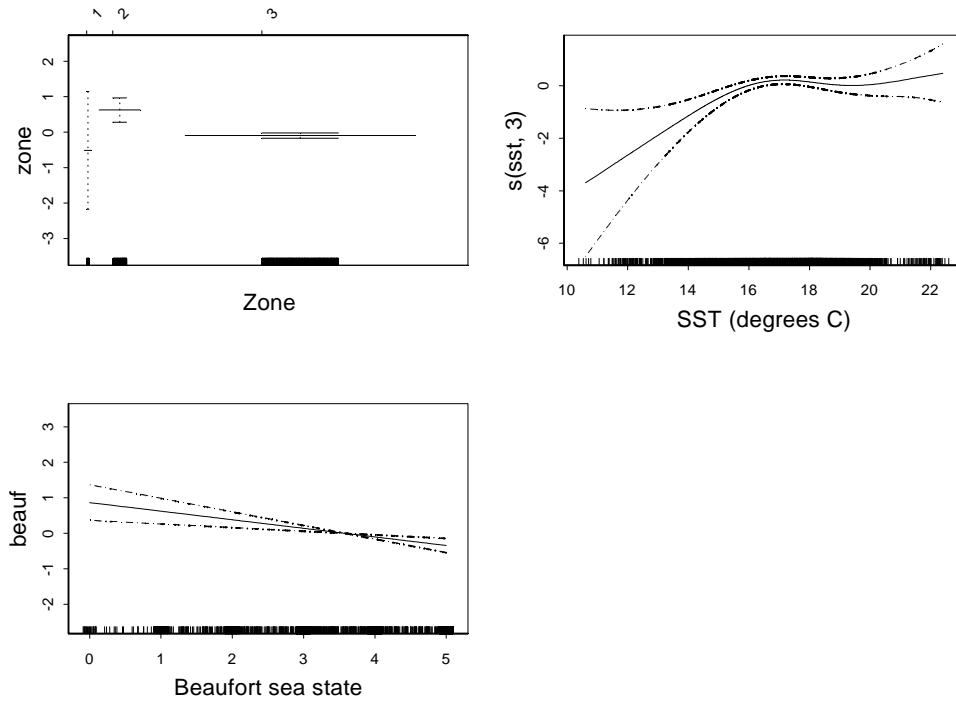


Group size GLM built with *in situ* data

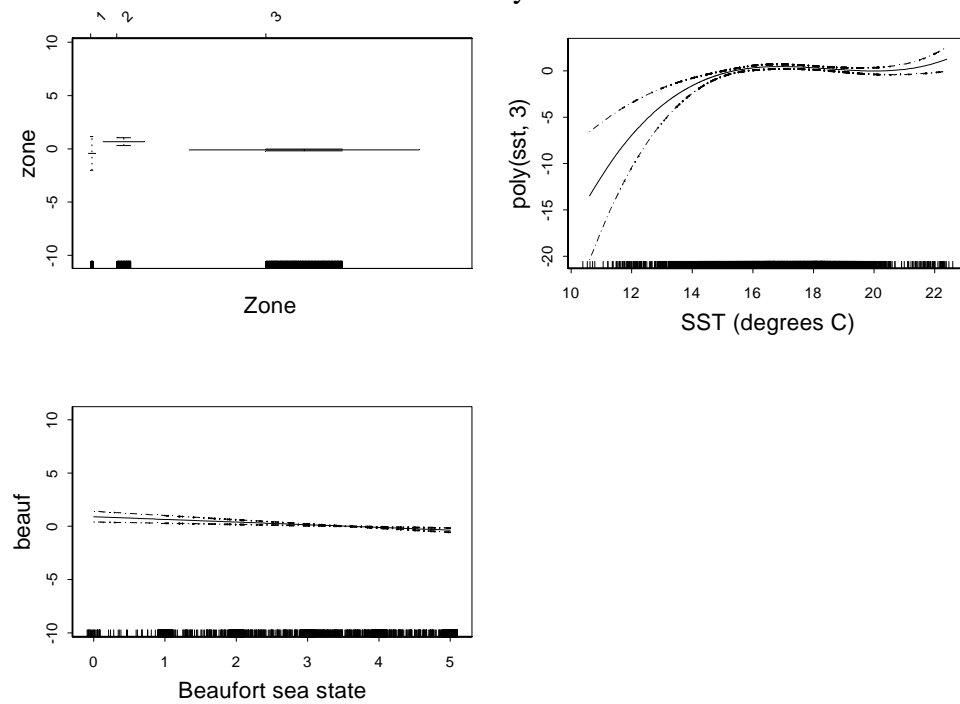


(b.1) Short-beaked common dolphin

Encounter rate GAM built with remotely sensed data

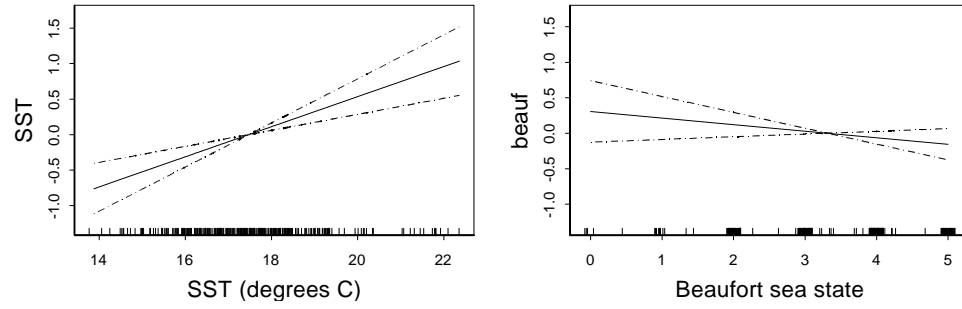


Encounter rate GLM built with remotely sensed data

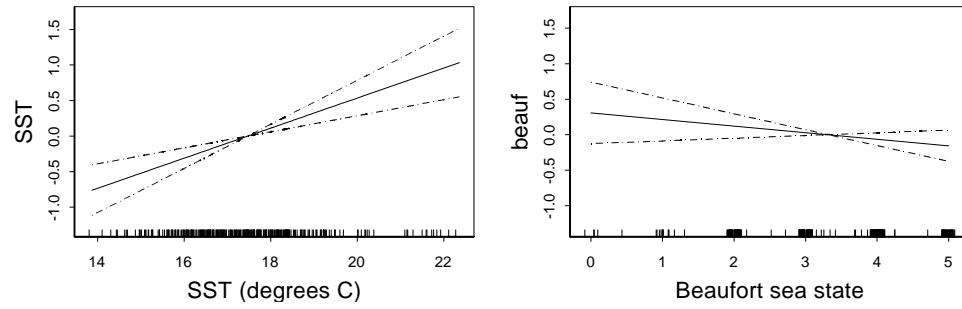


Short-beaked common dolphin (continued)

Group size GAM built with remotely sensed data

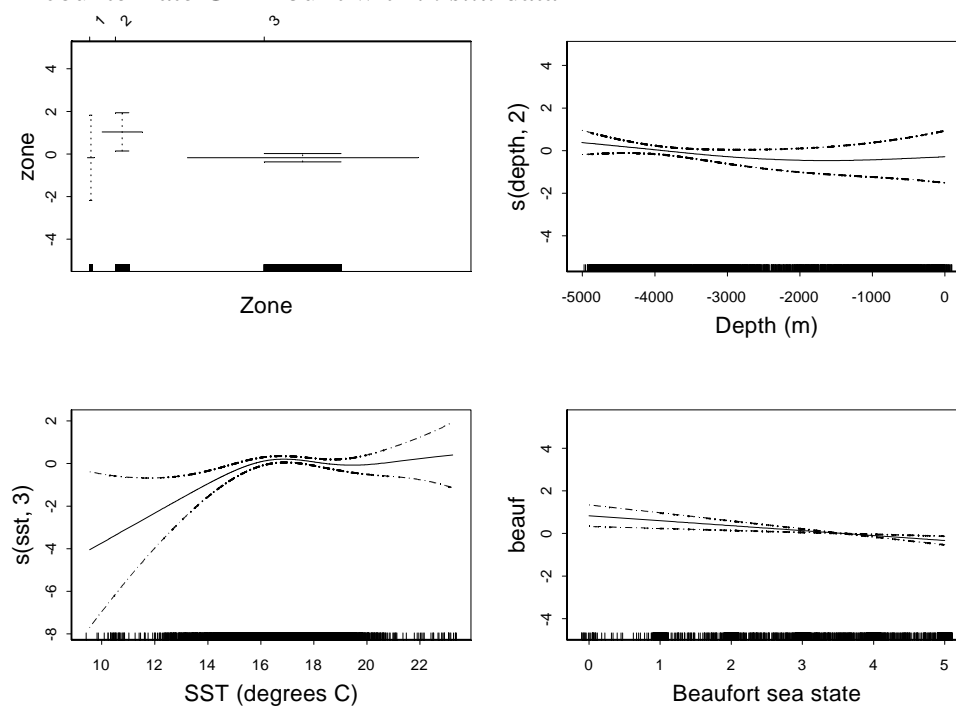


Group size GLM built with remotely sensed data

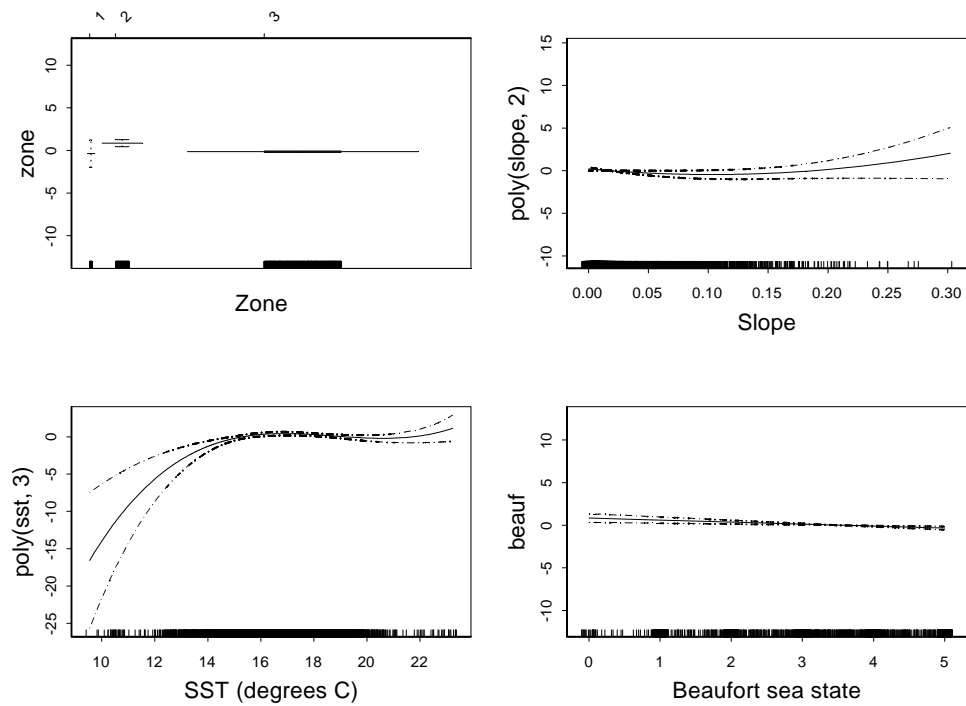


(b.2) Short-beaked common dolphin

Encounter rate GAM built with *in situ* data

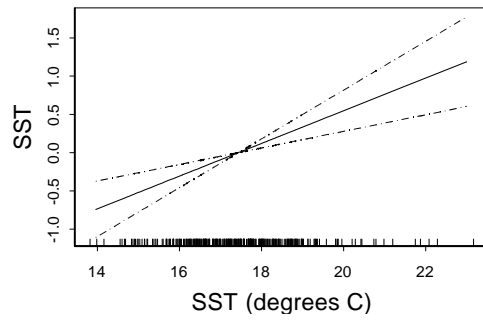


Encounter rate GLM built with *in situ* data

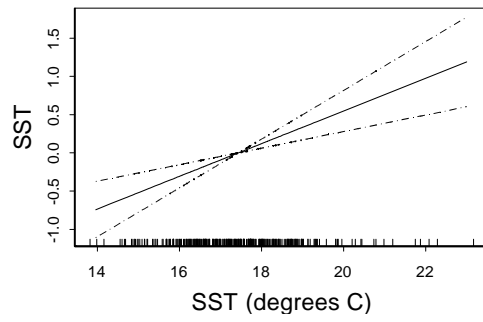


Short-beaked common dolphin (continued)

Group size GAM built with *in situ* data

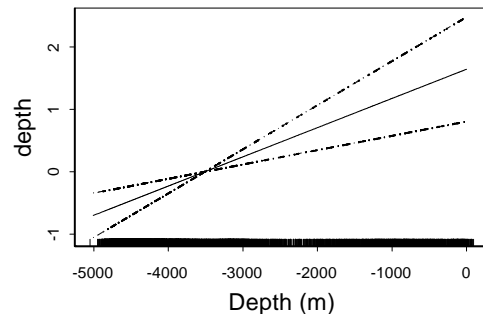


Group size GLM built with *in situ* data

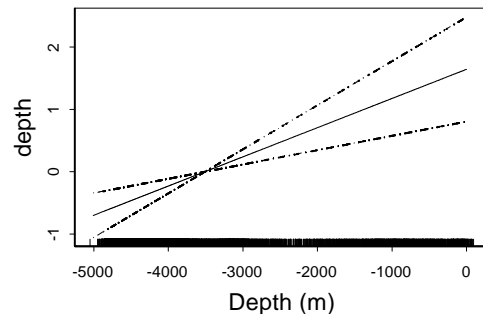


(c.1) Risso's dolphin

Encounter rate GAM built with remotely sensed data

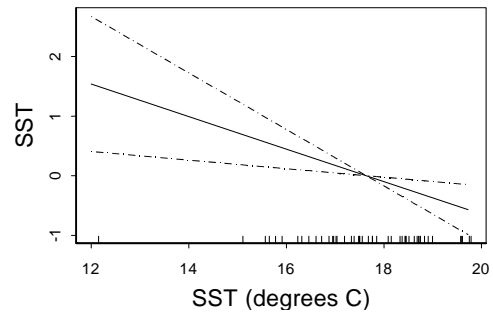


Encounter rate GLM built with remotely sensed data

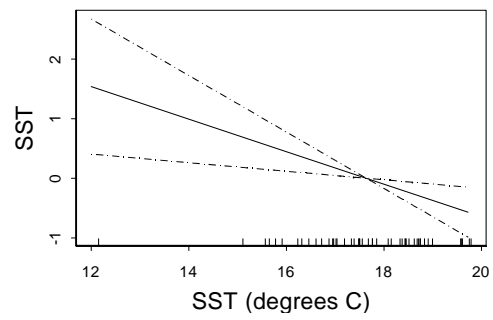


Risso's dolphin (continued)

Group size GAM built with remotely sensed data

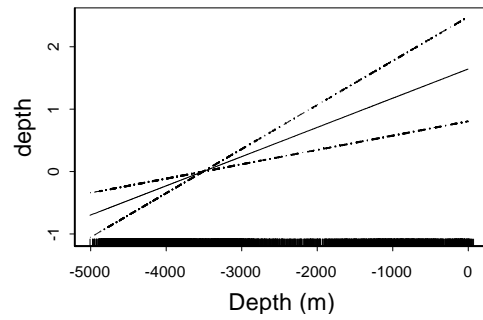


Group size GLM built with remotely sensed data

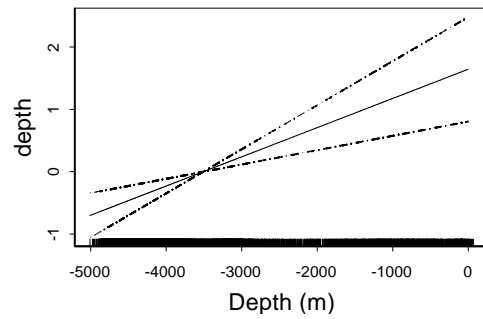


(c.2) Risso's dolphin

Encounter rate GAM built with *in situ* data

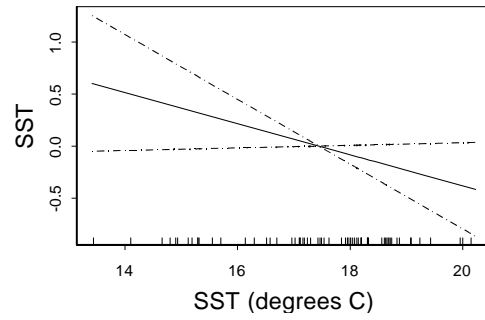


Encounter rate GLM built with *in situ* data

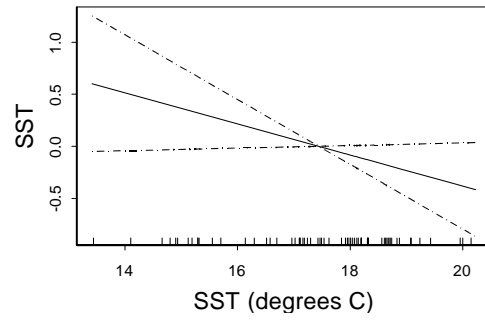


Risso's dolphin (continued)

Group size GAM built with *in situ* data

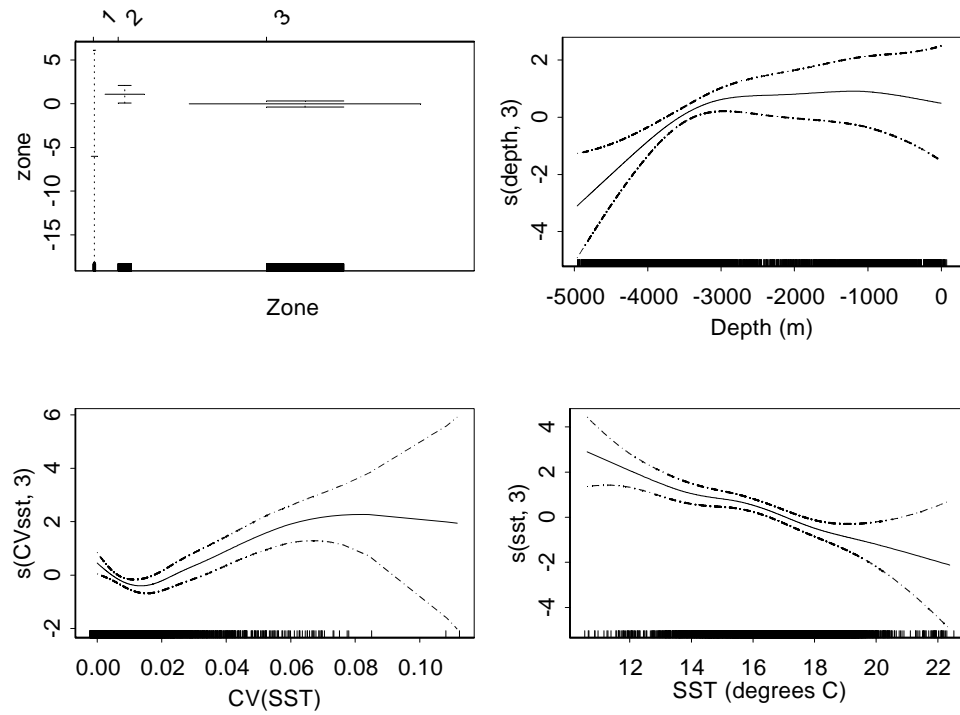


Group size GLM built with *in situ* data



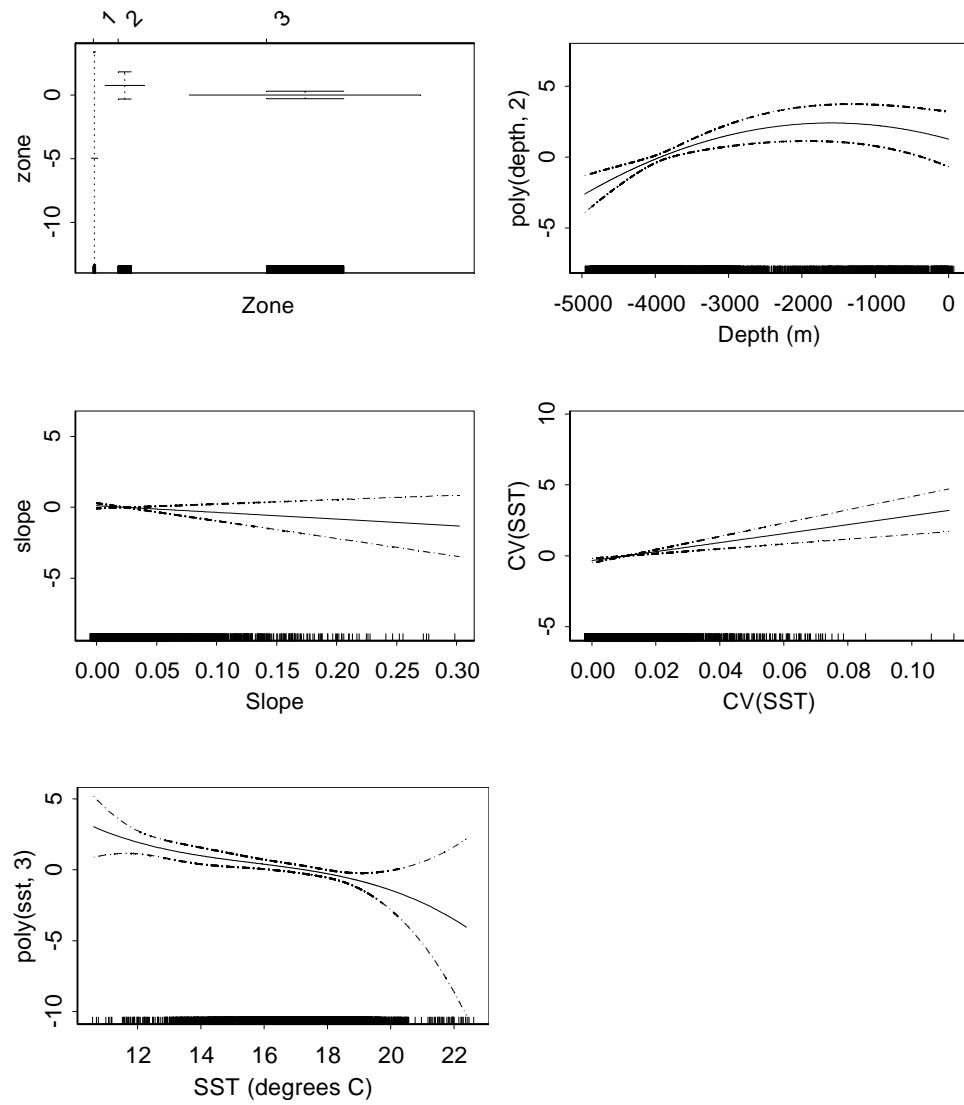
(d.1) Pacific white-sided dolphin

Encounter Rate GAM built with remotely sensed data



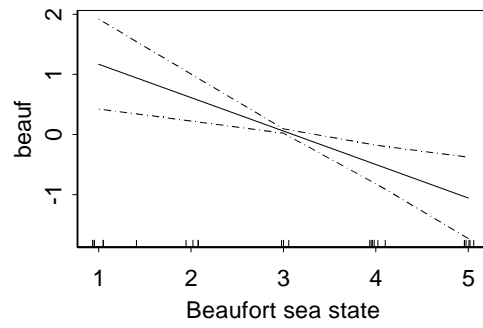
Pacific white-sided dolphin (continued)

Encounter Rate GLM built with remotely sensed data

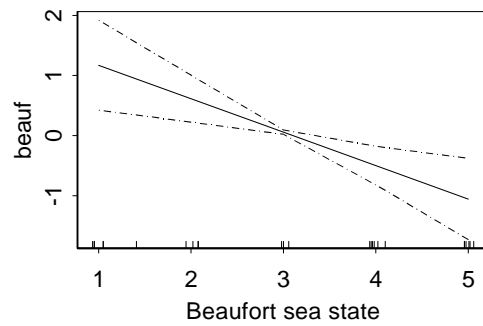


Pacific white-sided dolphin (continued)

Group size GAM built with remotely sensed data

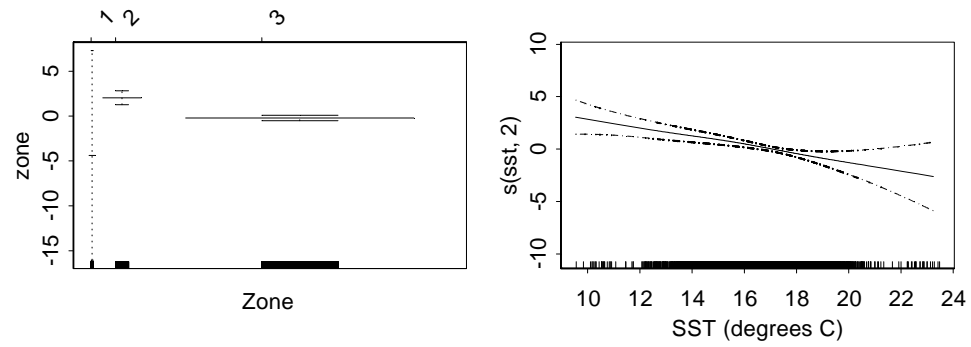


Group size GLM built with remotely sensed data

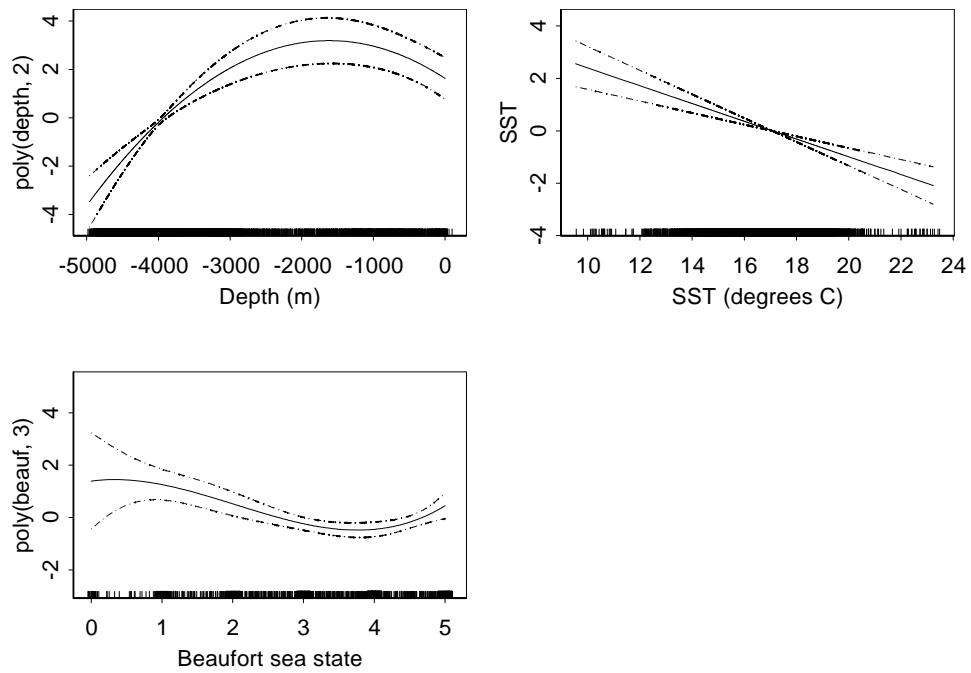


(d.2) Pacific white-sided dolphin

Encounter rate GAM built with *in situ* data

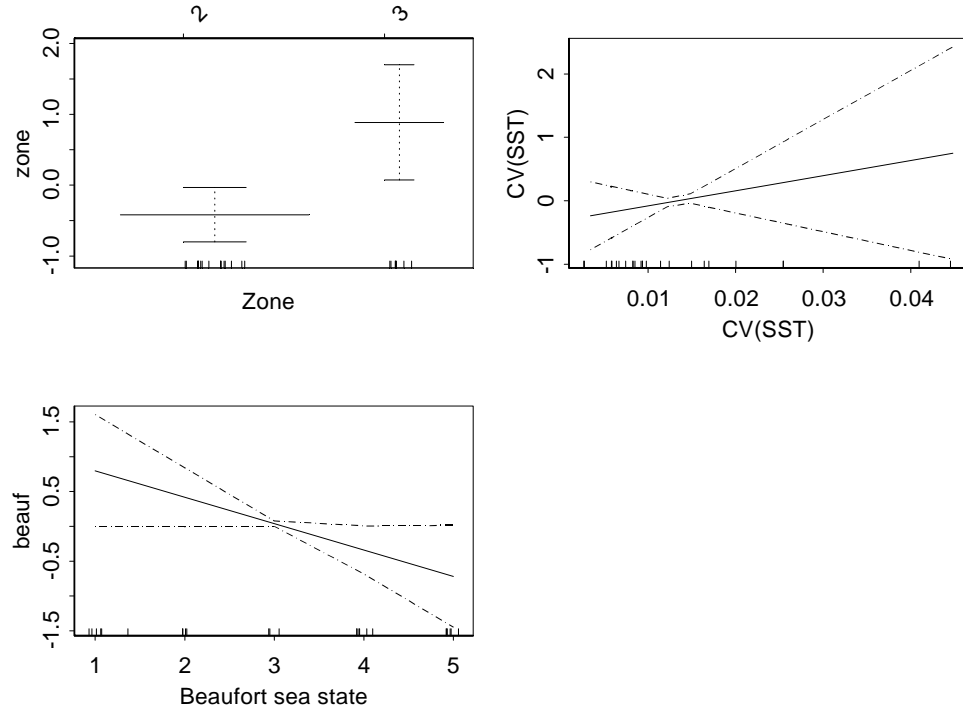


Encounter rate GLM built with *in situ* data

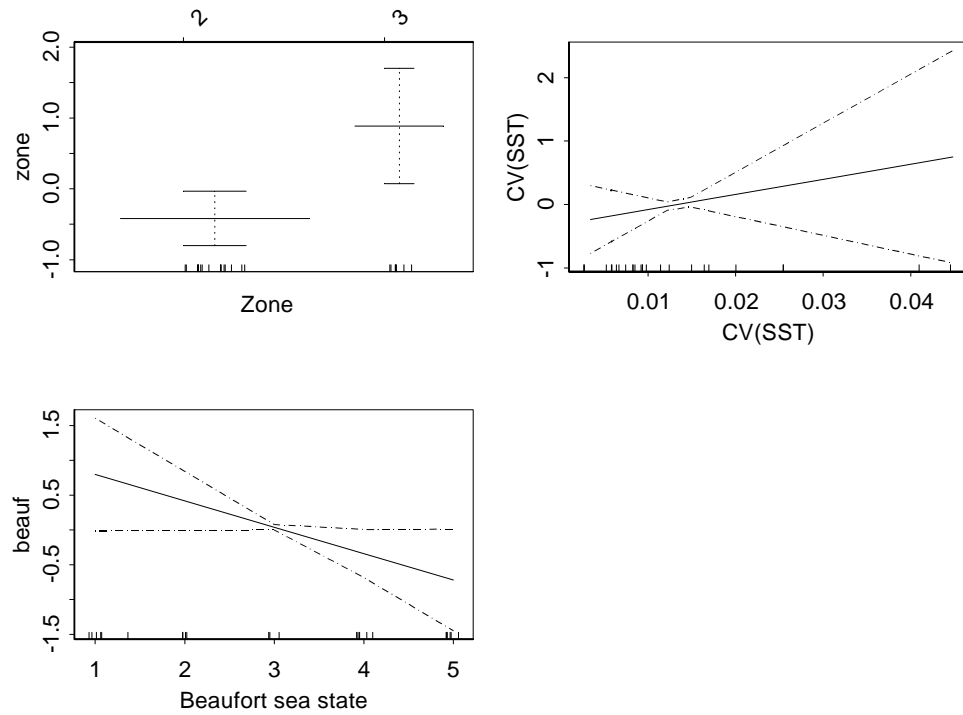


Pacific white-sided dolphin (continued)

Group size GAM built with *in situ* data

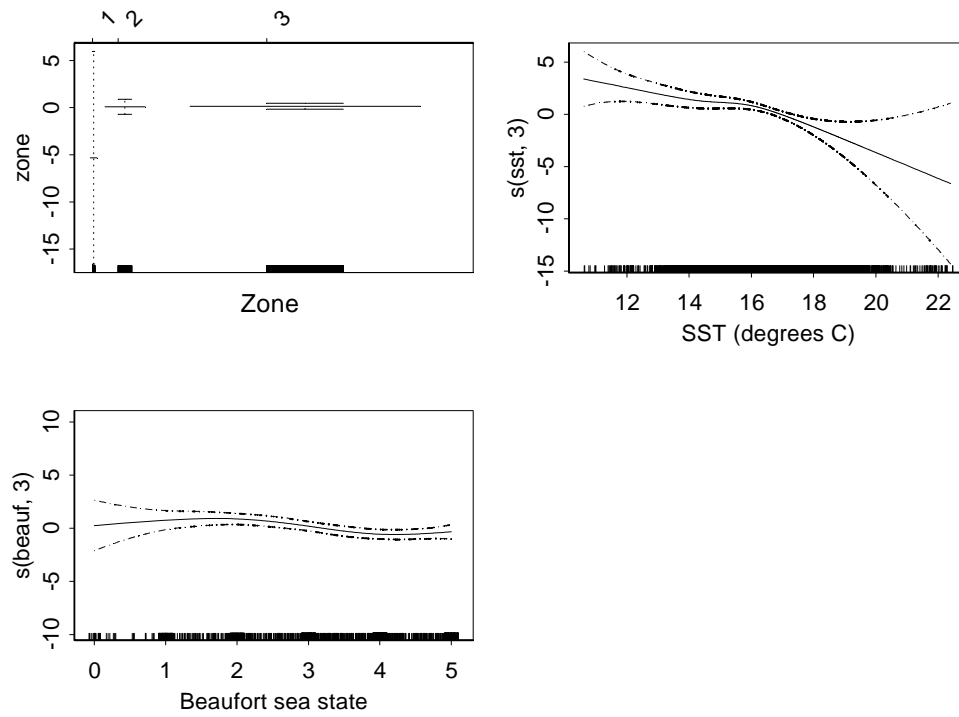


Group size GLM built with *in situ* data



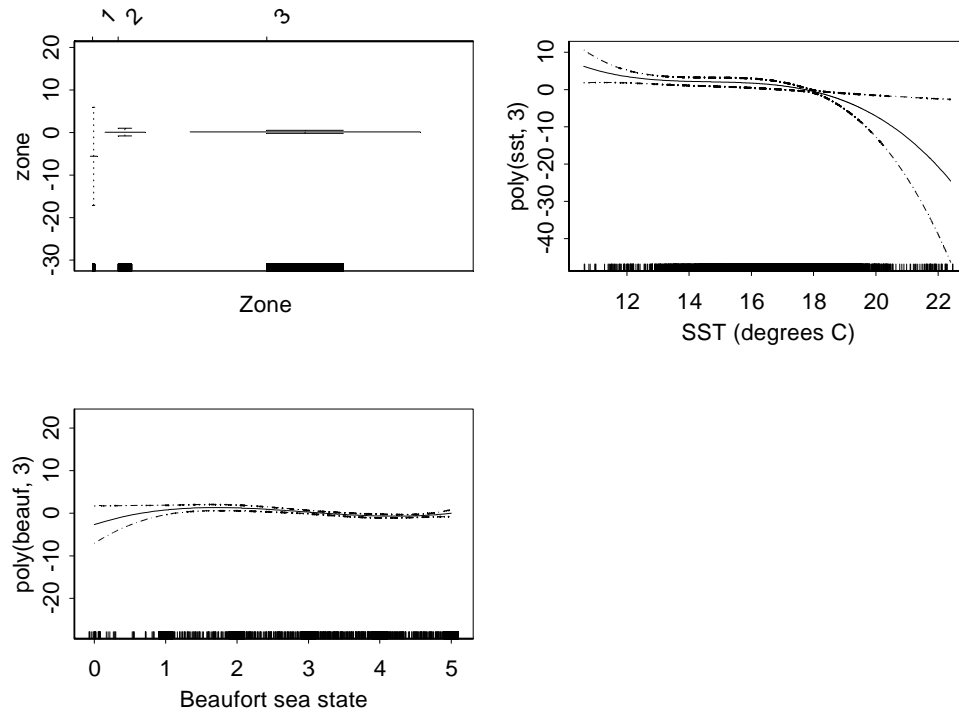
(e.1) Northern right whale dolphin

Encounter rate GAM built with remotely sensed data



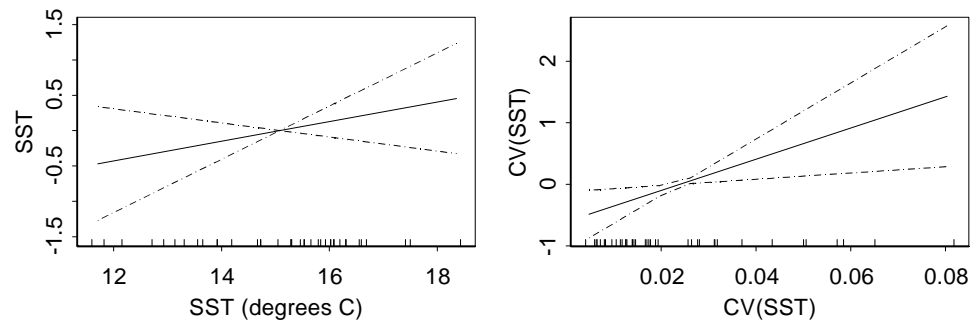
Northern right whale dolphin (continued)

Encounter rate GLM built with remotely sensed data

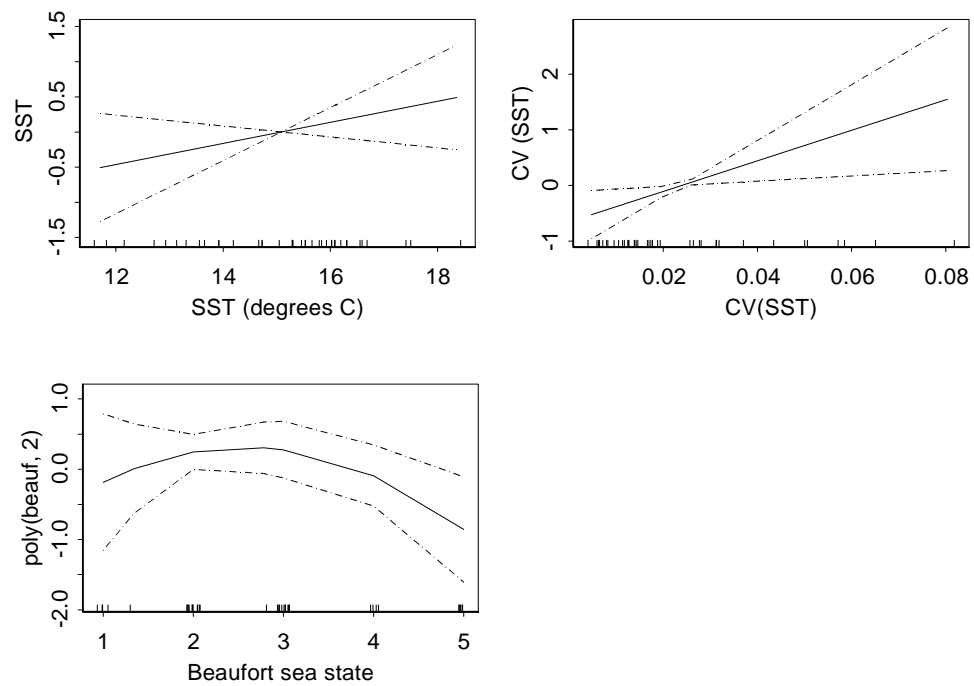


Northern right whale dolphin (continued)

Group size GAM built with remotely sensed data

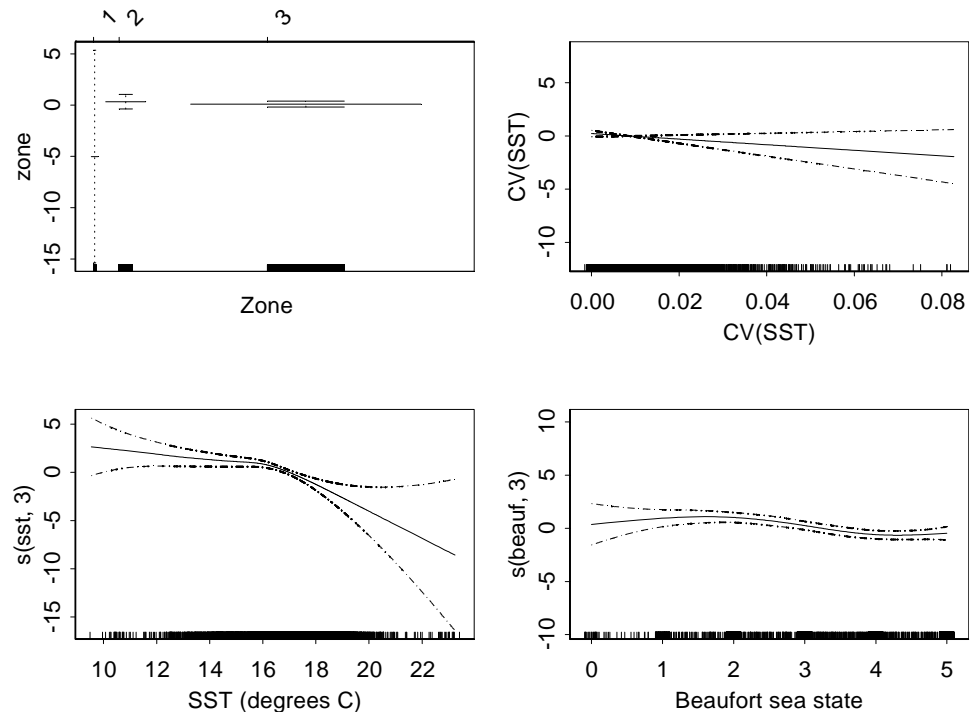


Group size GLM built with remotely sensed data



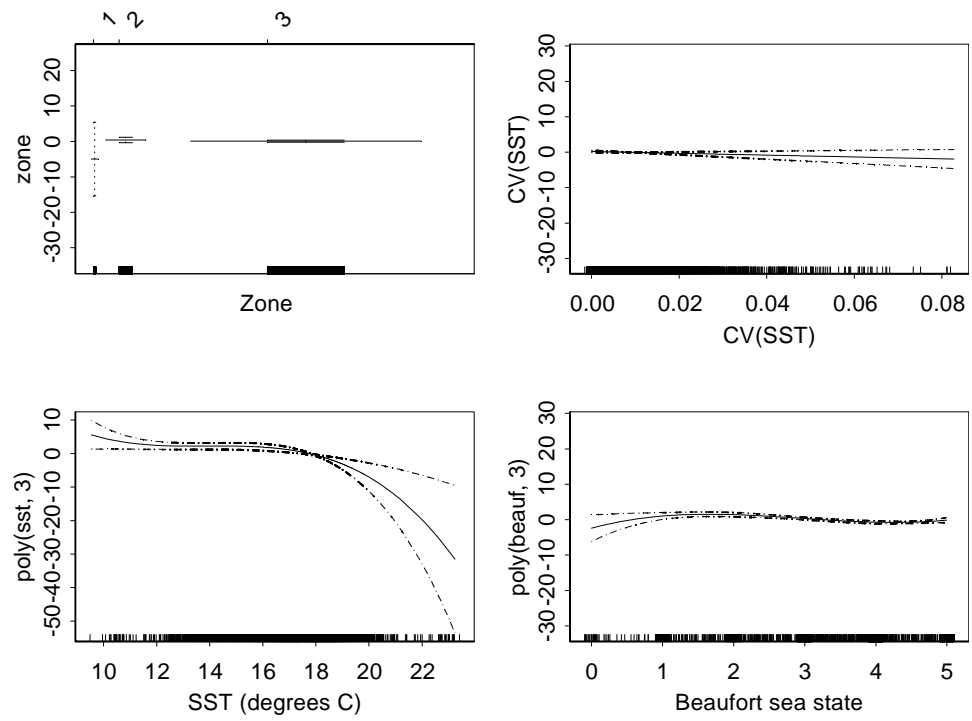
(e.2) Northern right whale dolphin

Encounter rate GAM built with *in situ* data



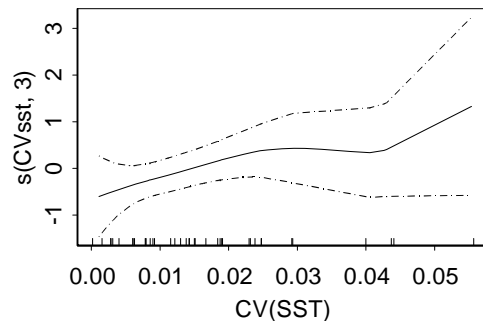
Northern right whale dolphin (continued)

Encounter rate GLM built with *in situ* data

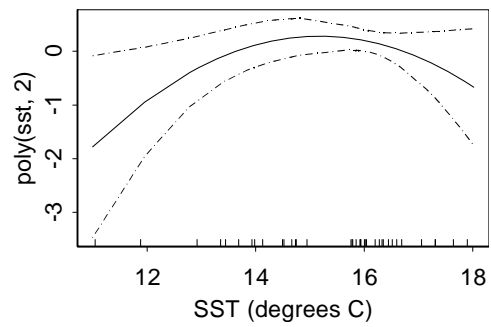


Northern right whale dolphin (continued)

Group size GAM built with *in situ* data

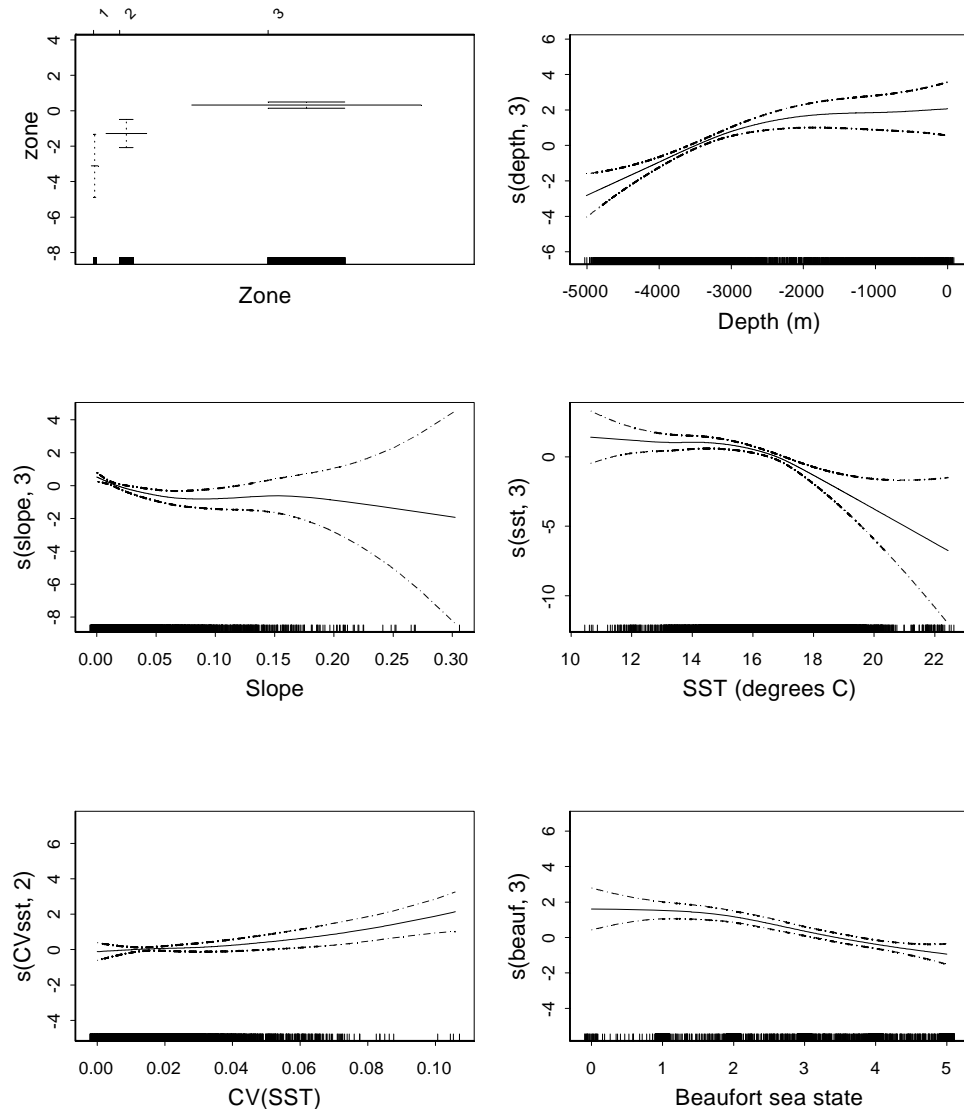


Group size GLM built with *in situ* data



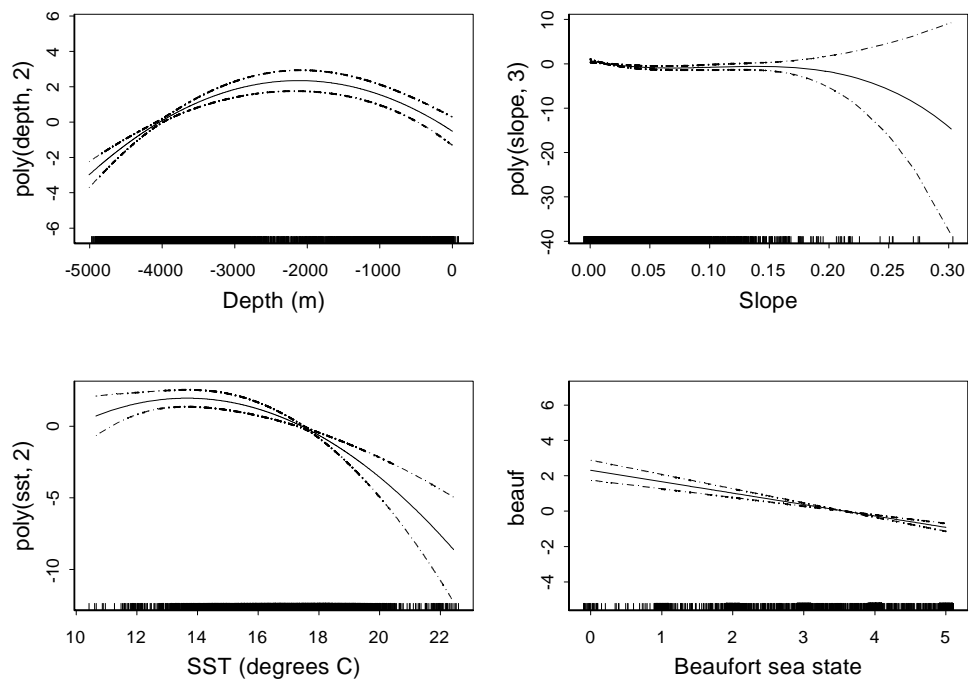
(f.1) Dall's porpoise

Encounter rate GAM built with remotely sensed data



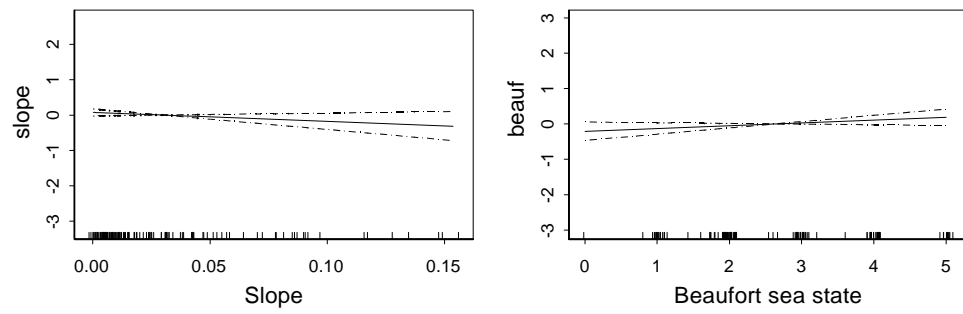
Dall's porpoise (continued)

Encounter rate GLM built with remotely sensed data

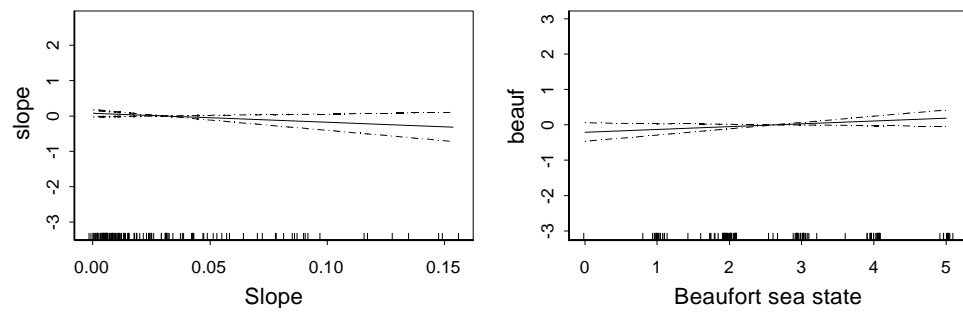


Dall's porpoise (continued)

Group size GAM built with remotely sensed data

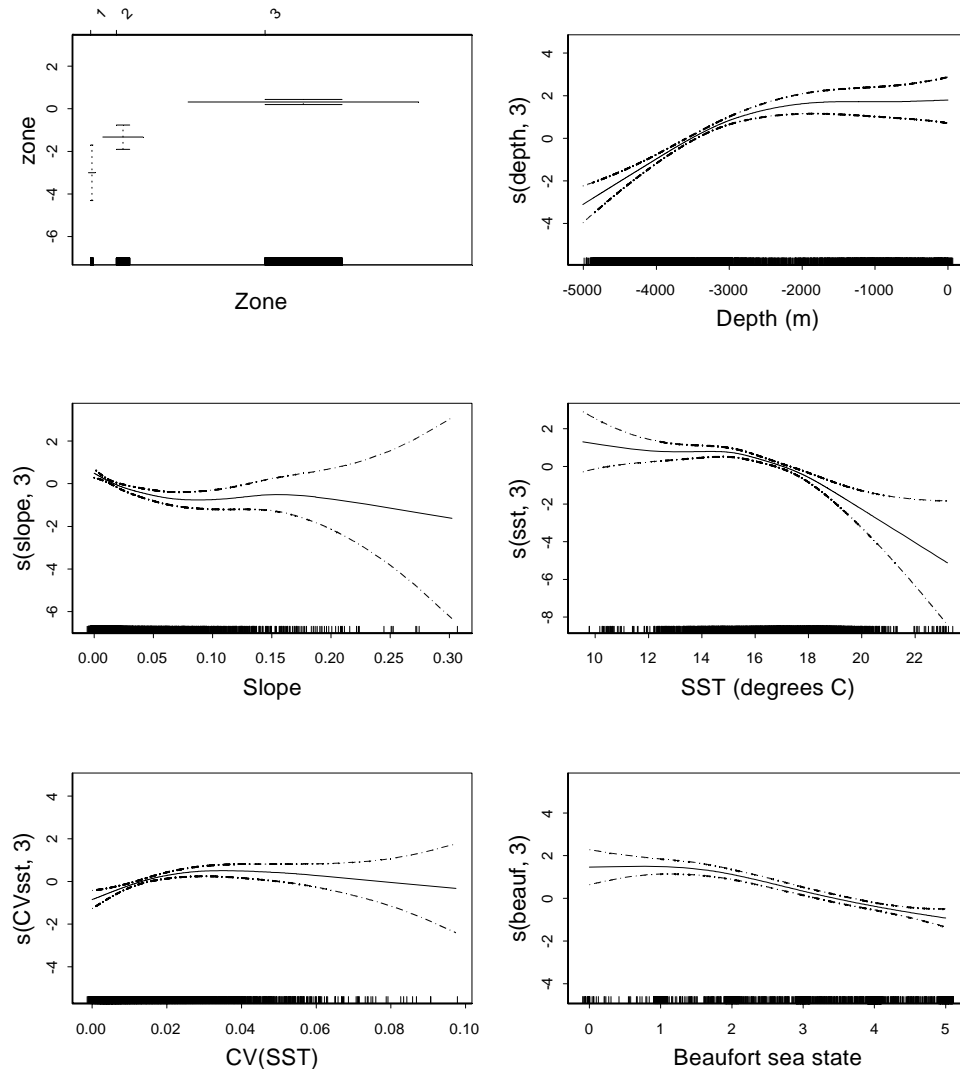


Group size GLM built with remotely sensed data



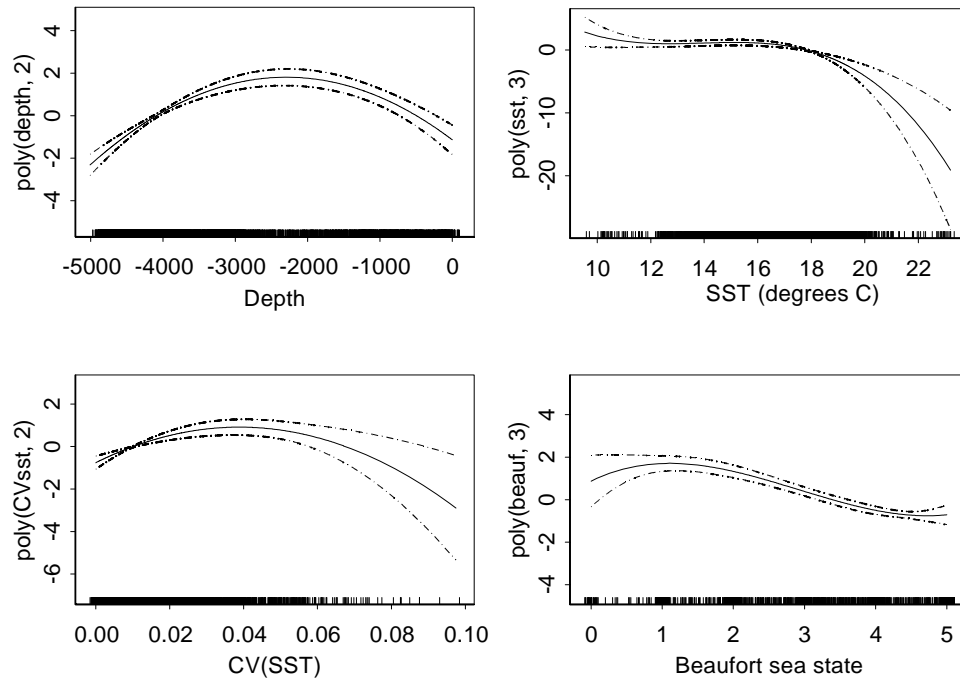
(f.2) Dall's porpoise

Encounter rate GAM built with *in situ* data

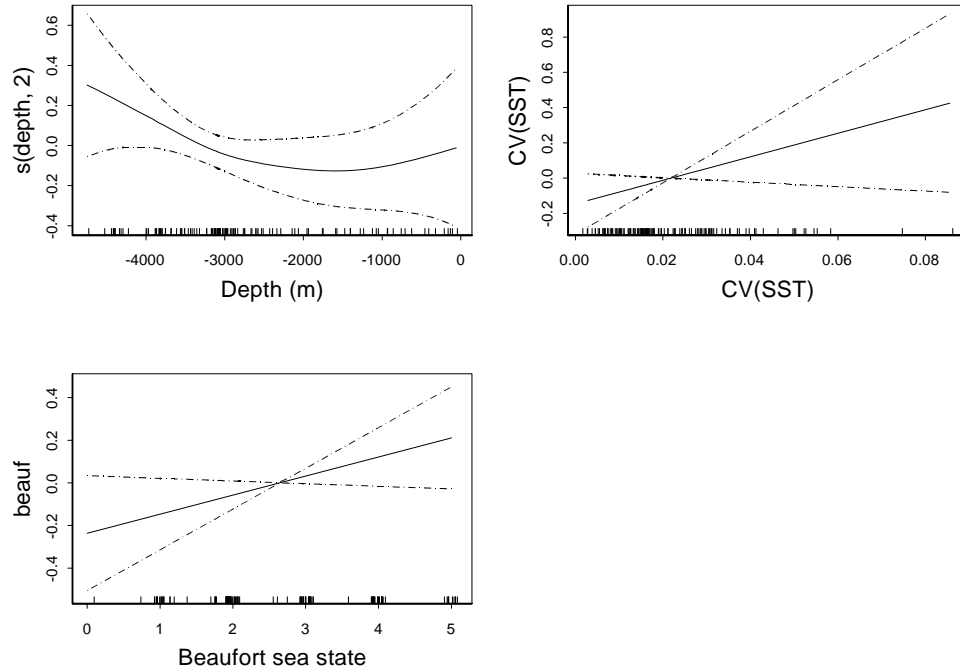


Dall's porpoise (continued)

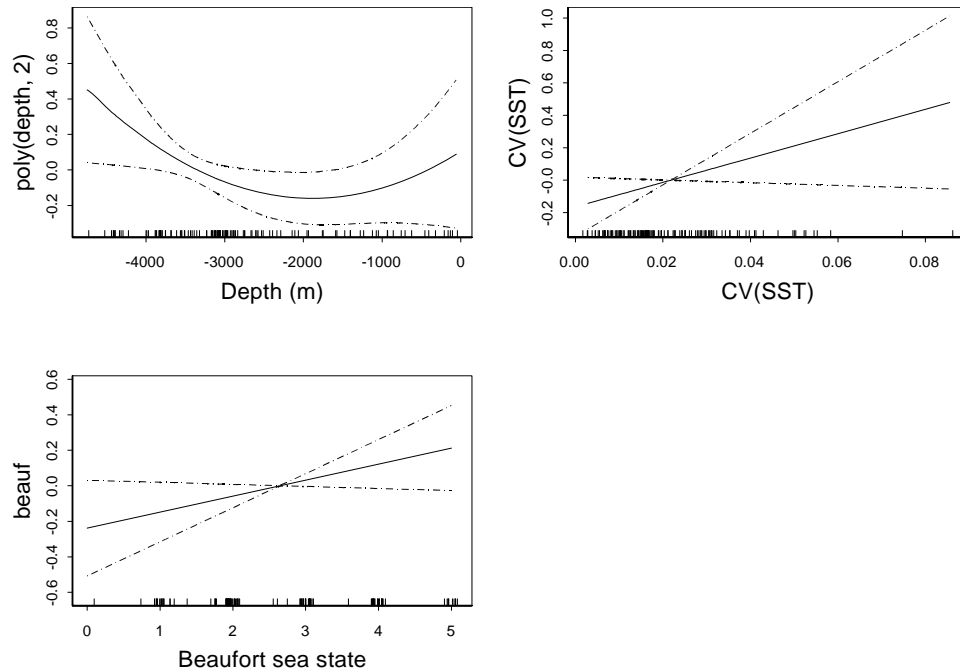
Encounter rate GLM built with *in situ* data



Dall's porpoise (continued)
Group size GAM built with *in situ* data

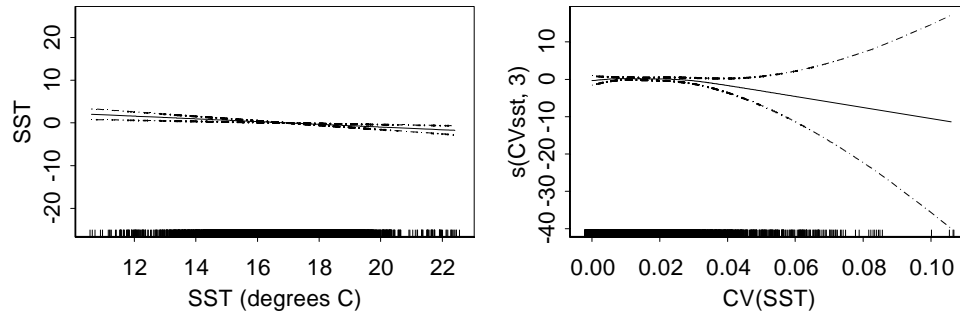


Group size GLM built with *in situ* data

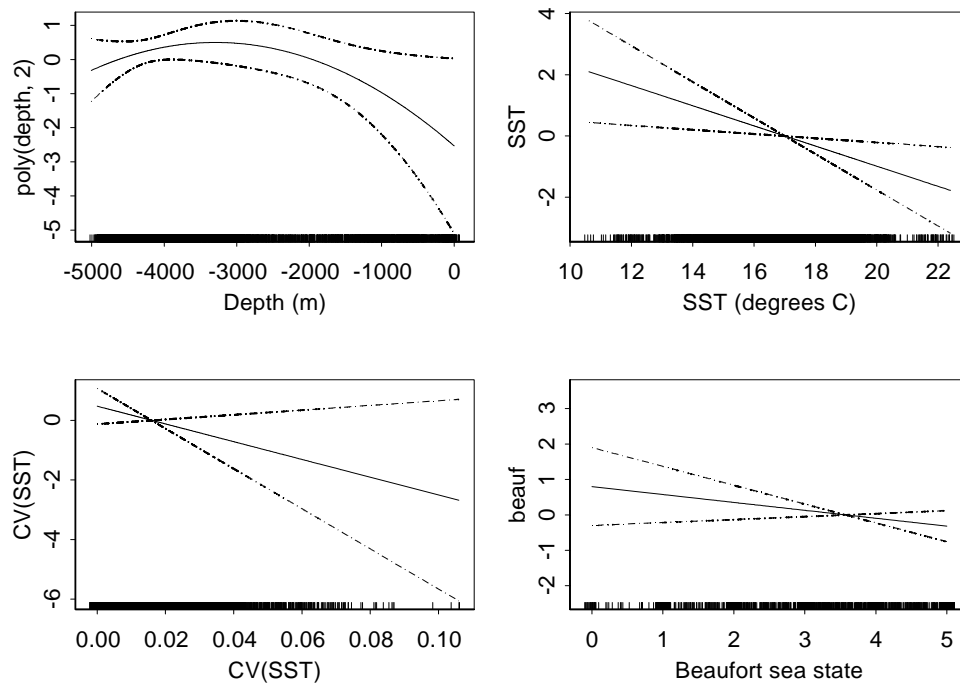


(g.1) Sperm whale

Encounter rate GAM built with remotely sensed data

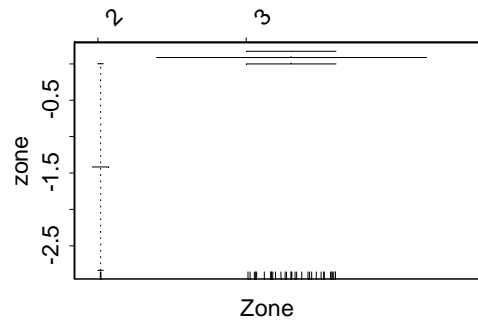


Encounter rate GLM built with remotely sensed data

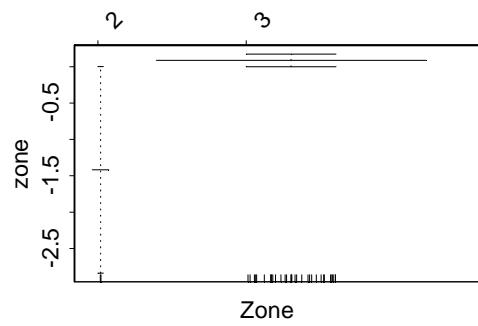


Sperm whale (continued)

Group size GAM built with remotely sensed data

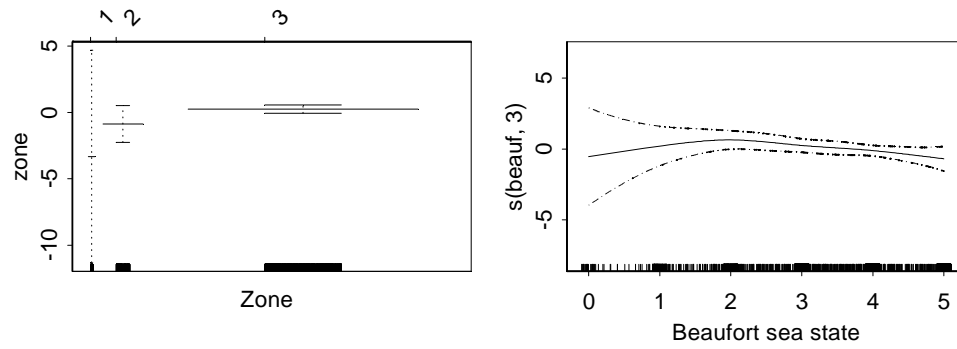


Group size GLM built with remotely sensed data

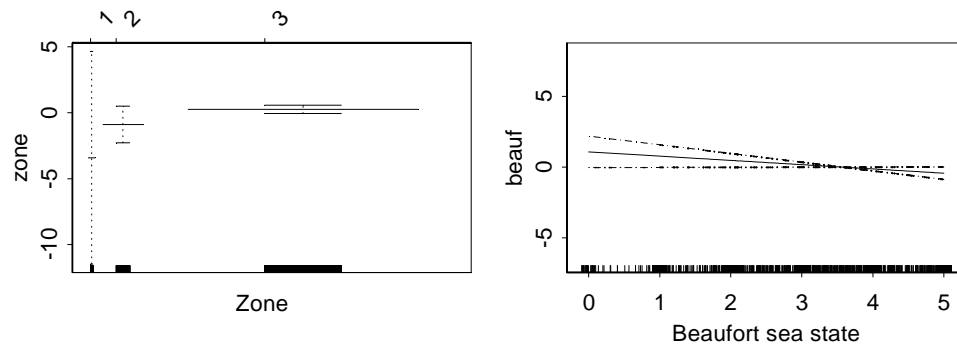


(g.2) Sperm whale

Encounter rate GAM built with *in situ* data

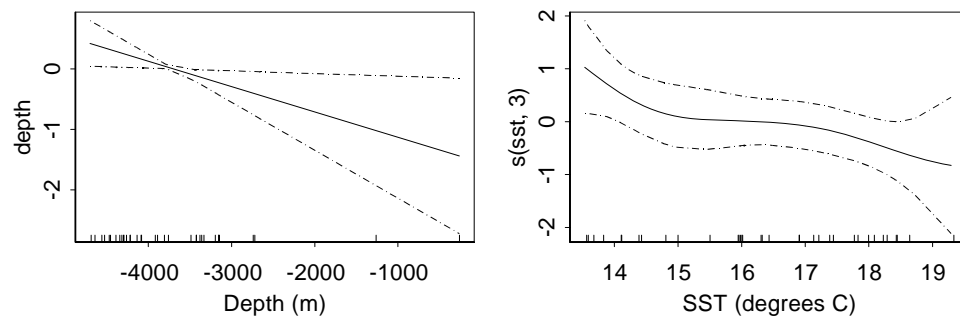


Encounter rate GLM built with *in situ* data

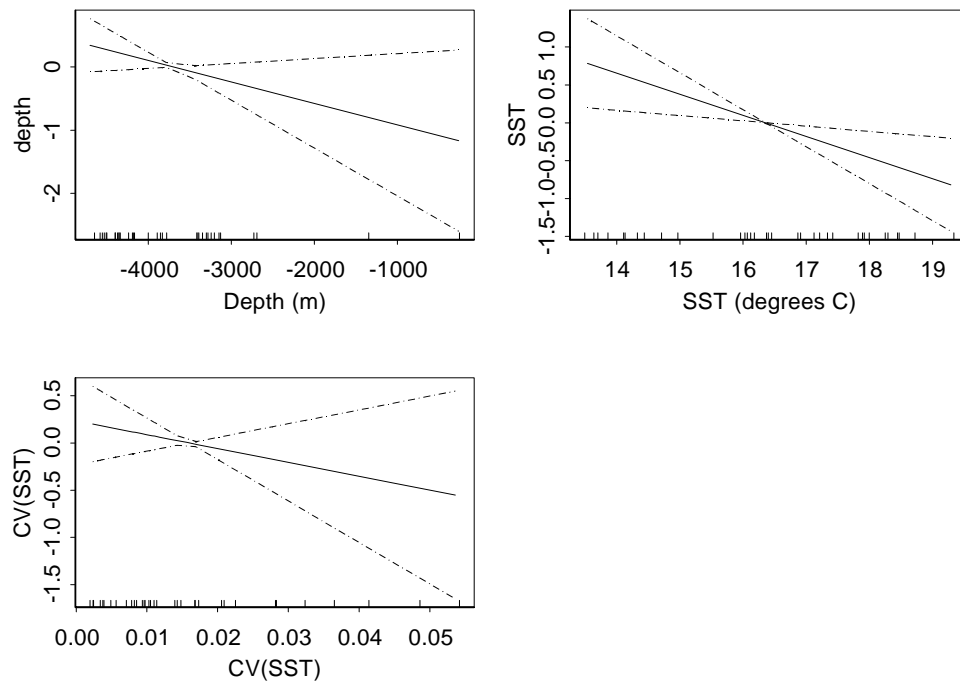


Sperm whale (continued)

Group size GAM built with *in situ* data

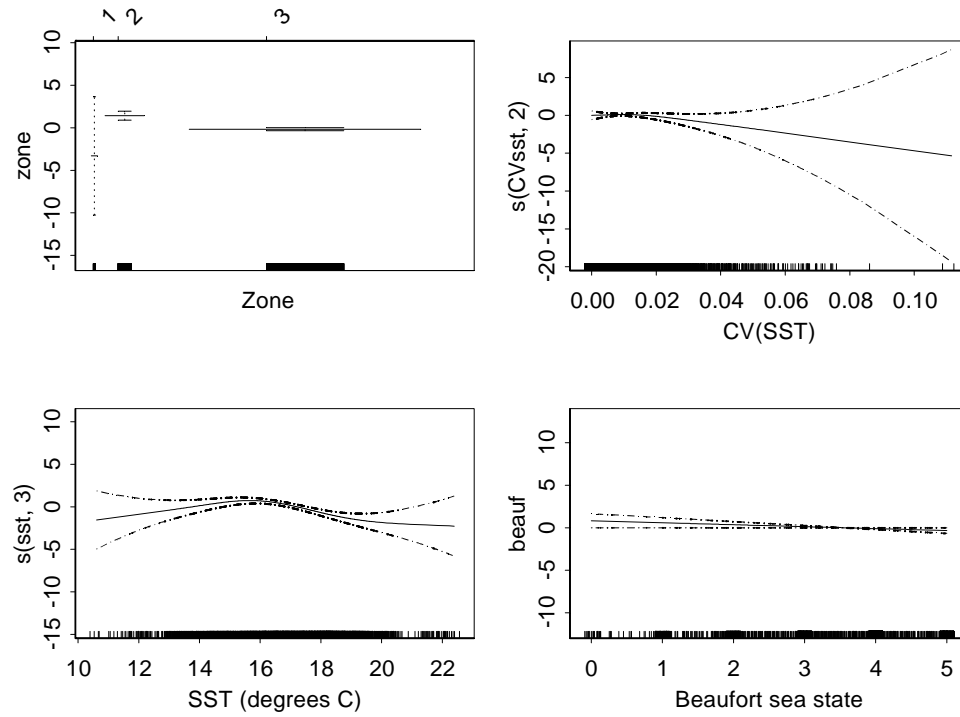


Group size GLM built with *in situ* data

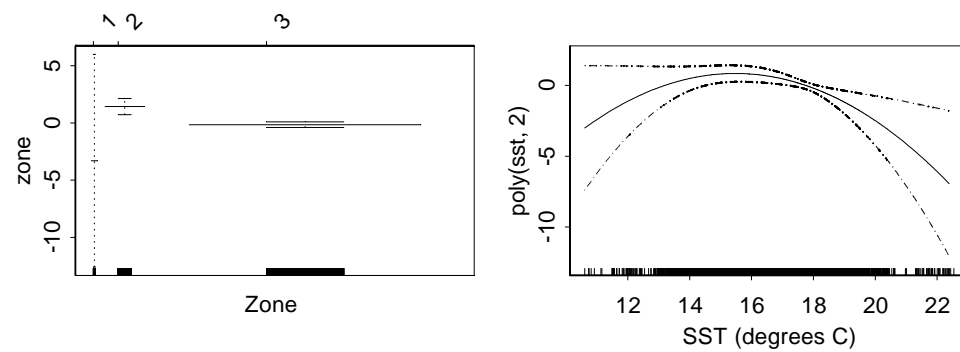


(h.1) Fin whale

Encounter rate GAM built with remotely sensed data

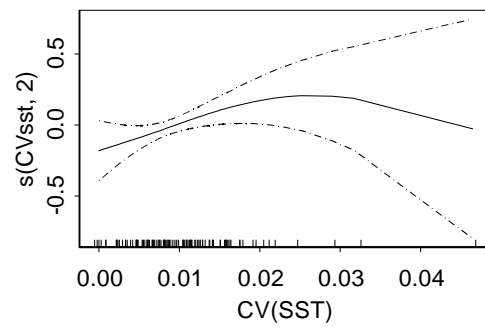


Encounter rate GLM built with remotely sensed data

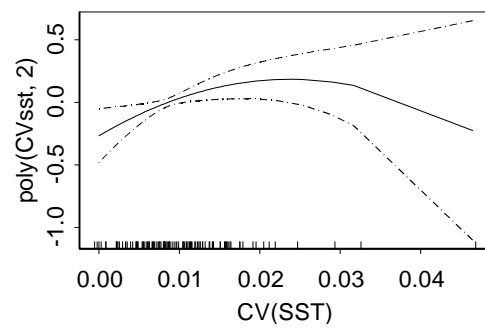


Fin whale (continued)

Group size GAM built with remotely sensed data

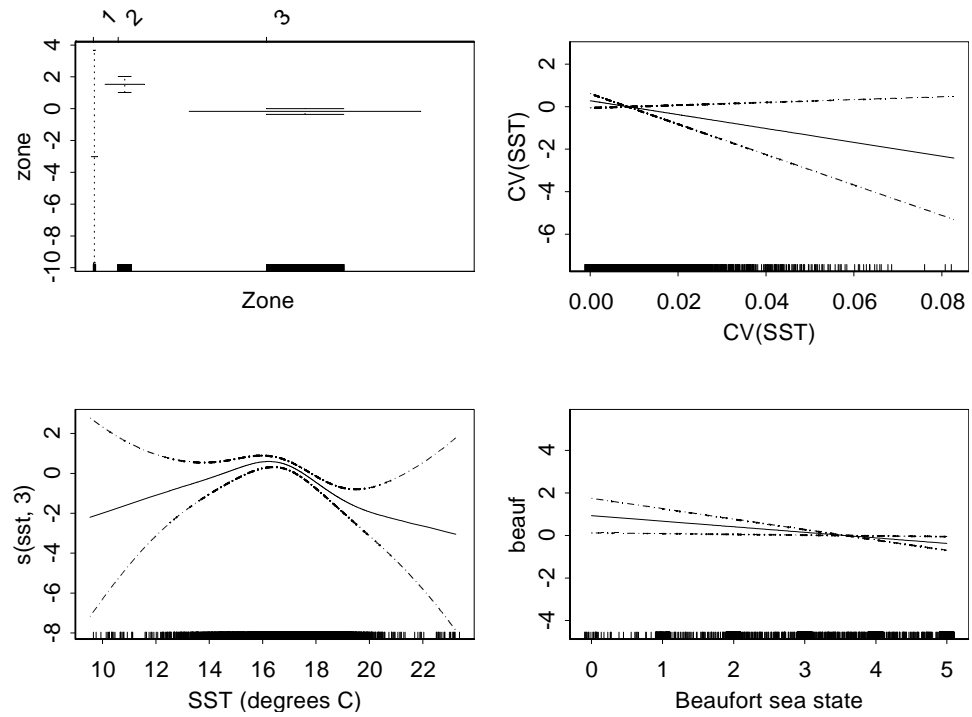


Group size GLM built with remotely sensed data

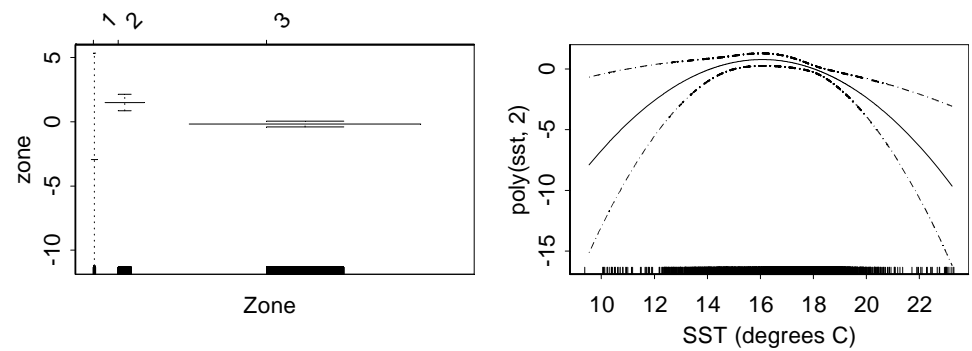


(h.2) Fin whale

Encounter rate GAM built with *in situ* data

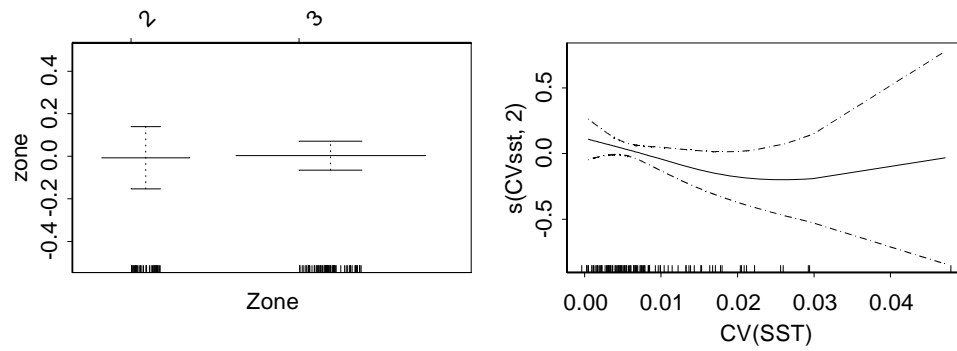


Encounter rate GLM built with *in situ* data

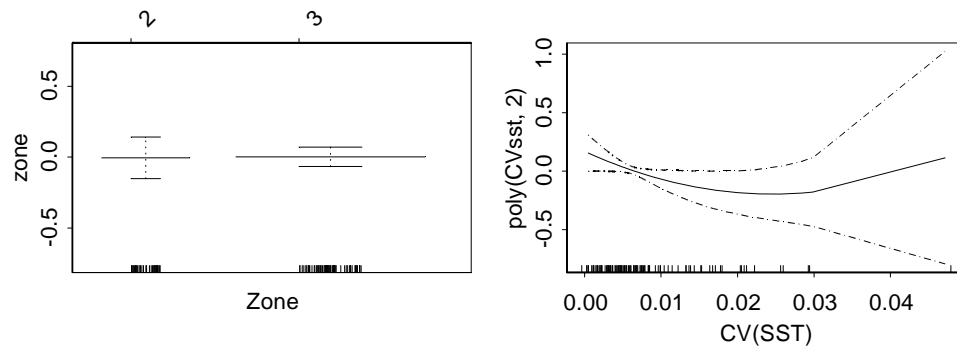


Fin whale (continued)

Group size GAM built with *in situ* data

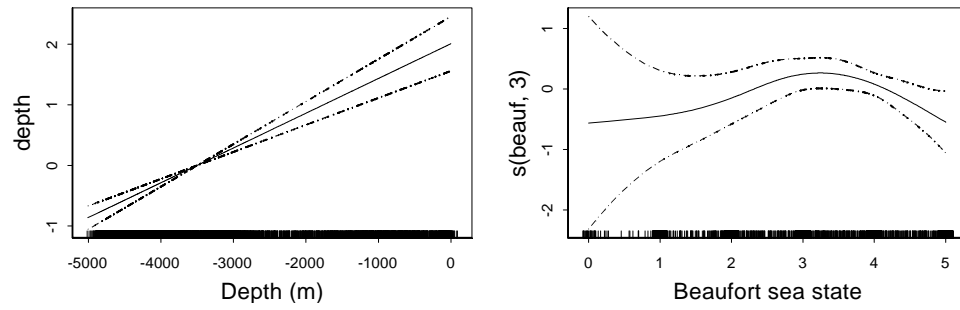


Group size GLM built with *in situ* data

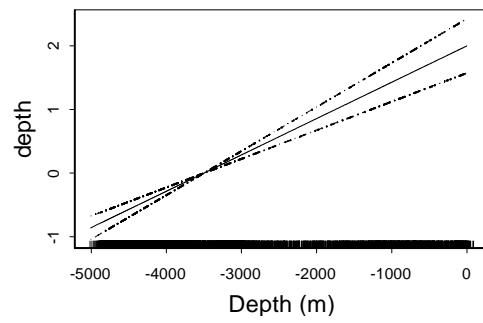


(i.1) Blue whale

Encounter rate GAM built with remotely sensed data

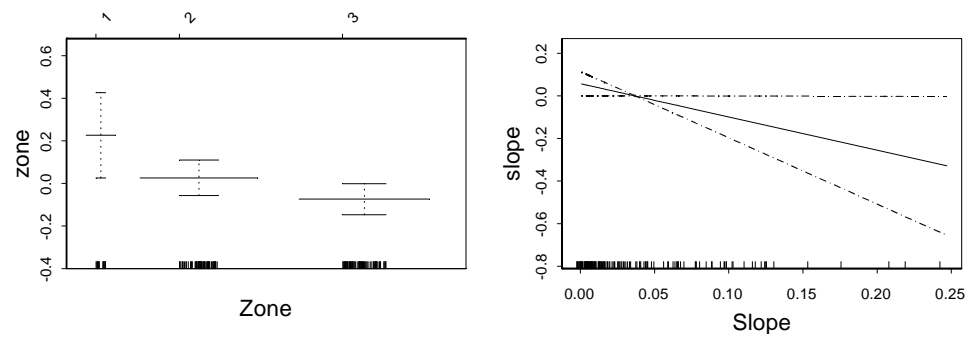


Encounter rate GLM built with remotely sensed data

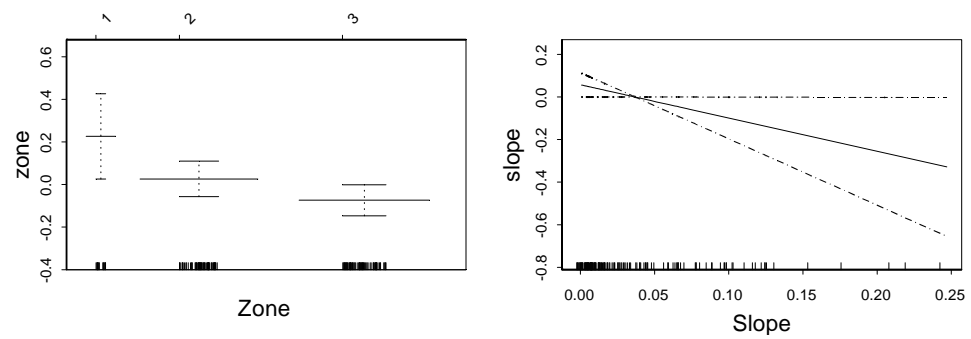


Blue whale (continued)

Group size GAM built with remotely sensed data

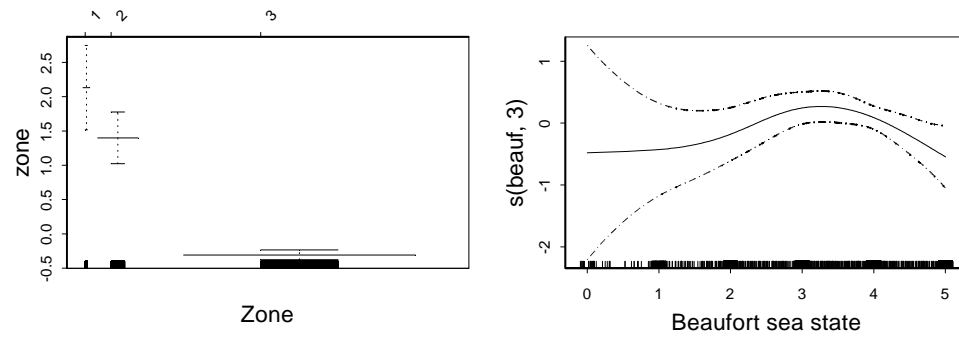


Group size GLM built with remotely sensed data

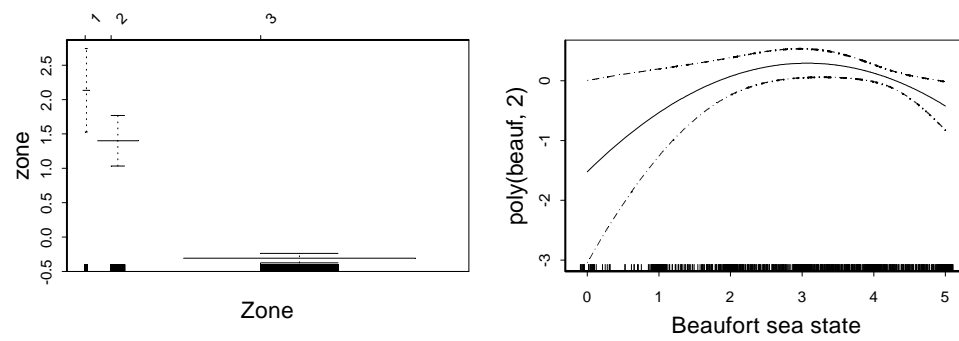


(i.2) Blue whale

Encounter rate GAM built with *in situ* data

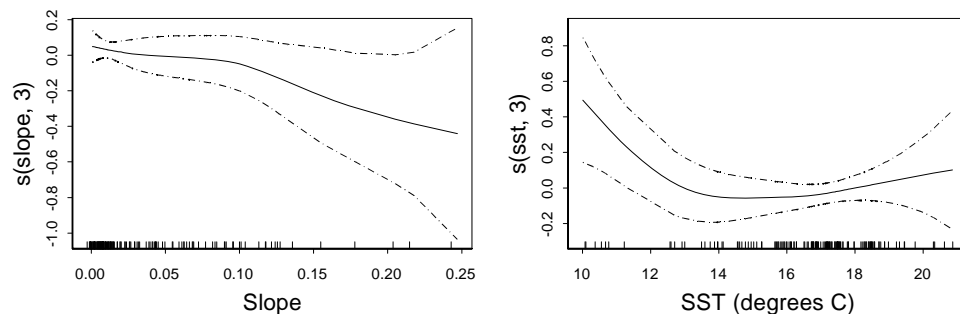


Encounter rate GLM built with *in situ* data

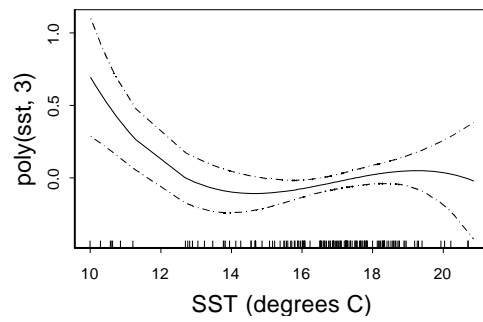


Blue whale (continued)

Group size GAM built with *in situ* data

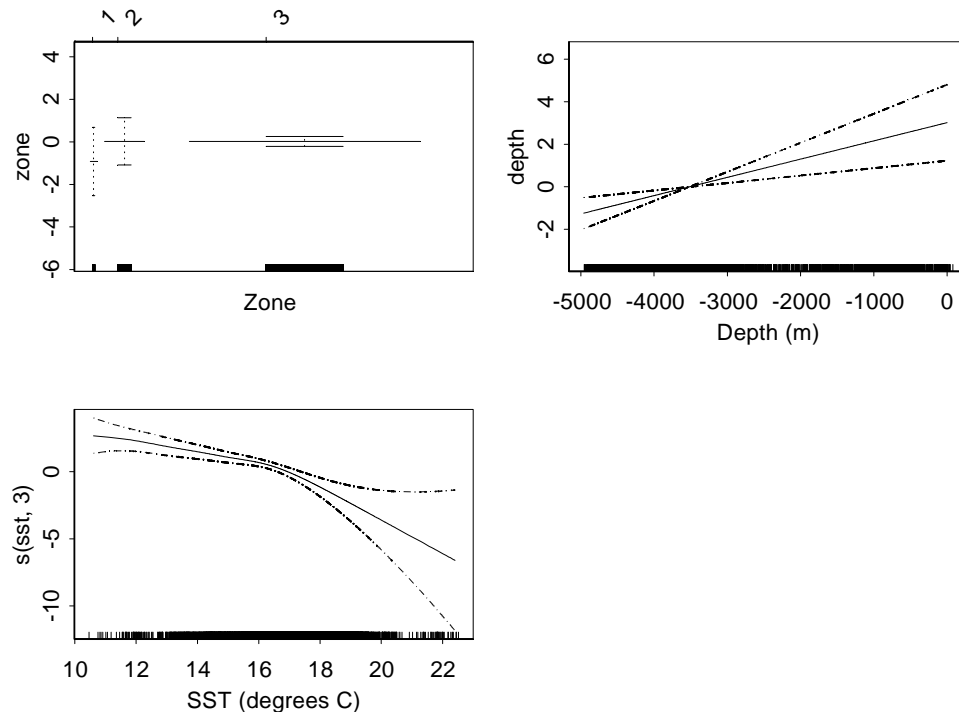


Group size GLM built with *in situ* data

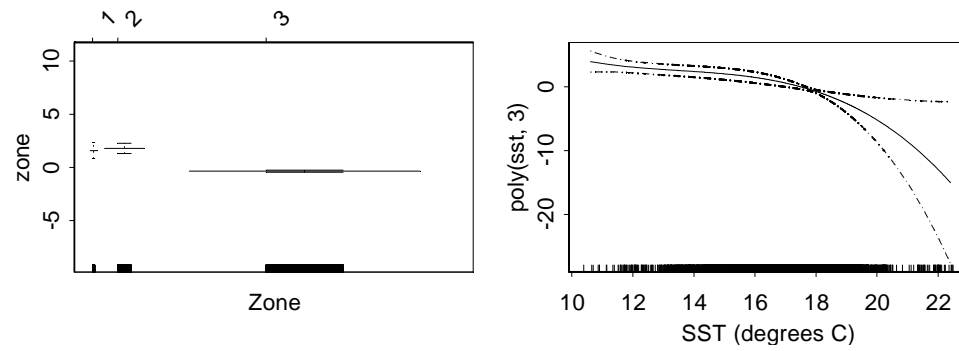


(j.1) Humpback whale

Encounter rate GAM built with remotely sensed data

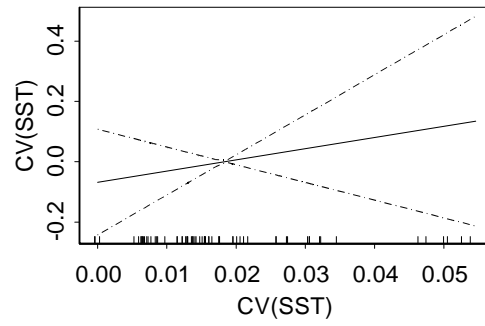


Encounter rate GLM built with remotely sensed data

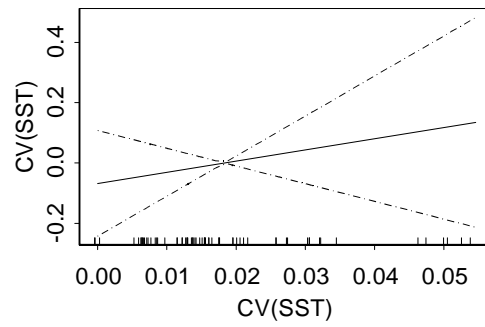


Humpback whale (continued)

Group size GAM built with remotely sensed data

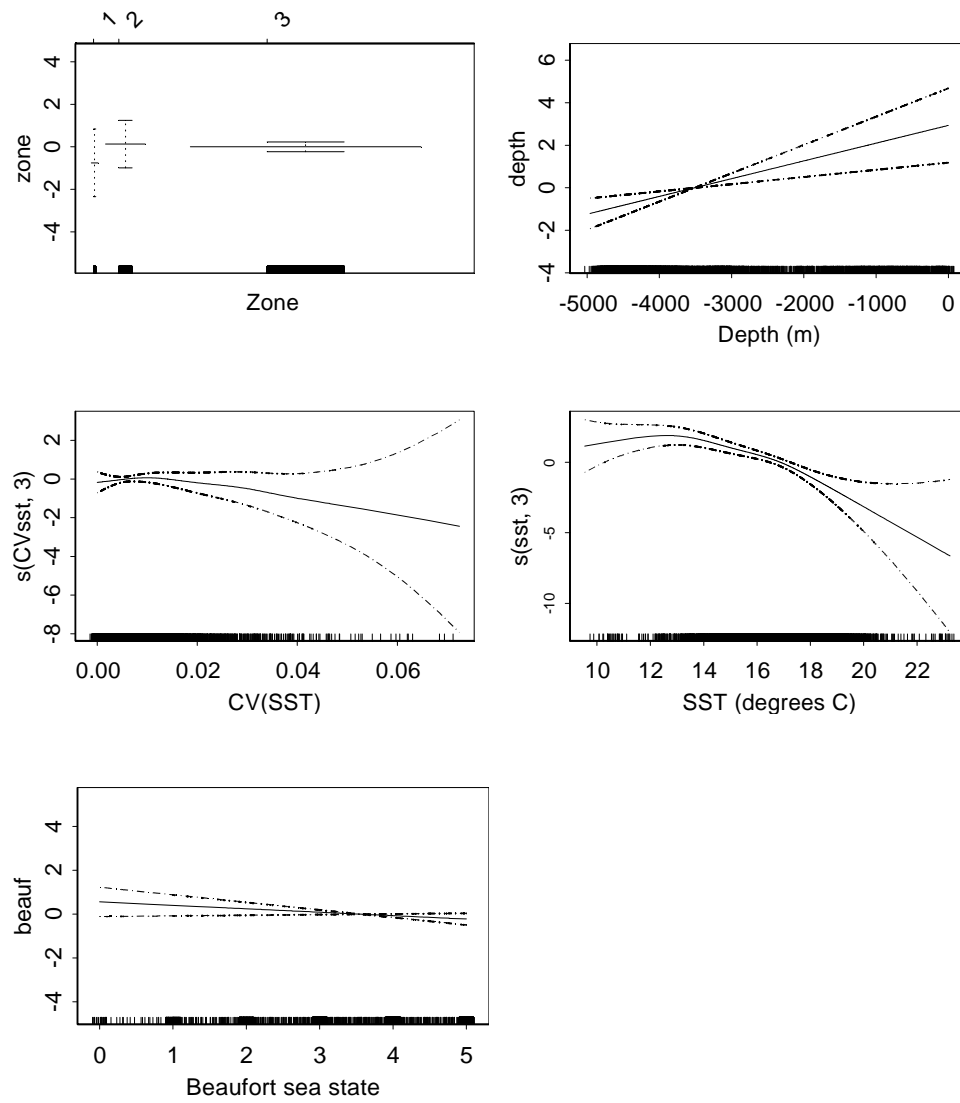


Group size GLM built with remotely sensed data



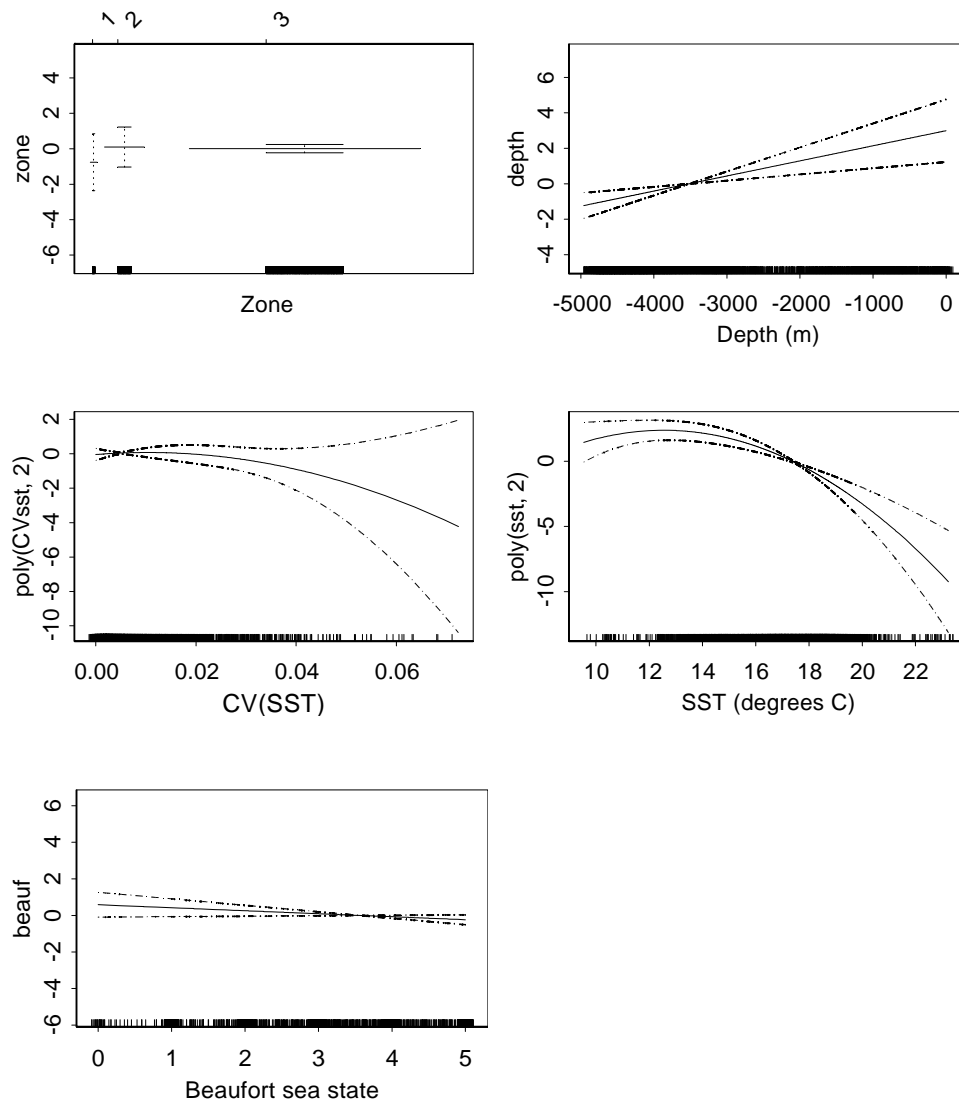
(j.2) Humpback whale

Encounter rate GAM built with *in situ* data



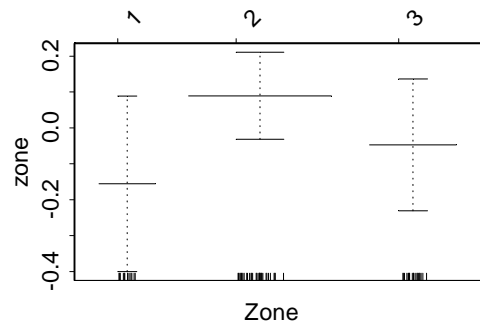
Humpback whale (continued)

Encounter rate GLM built with *in situ* data

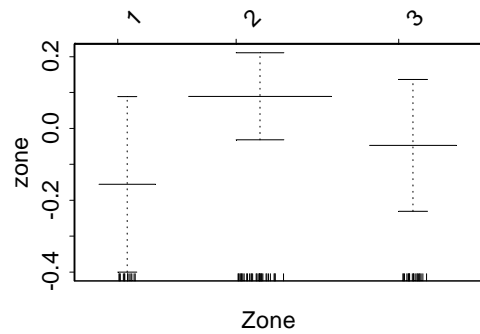


Humpback whale (continued)

Group size GAM built with *in situ* data



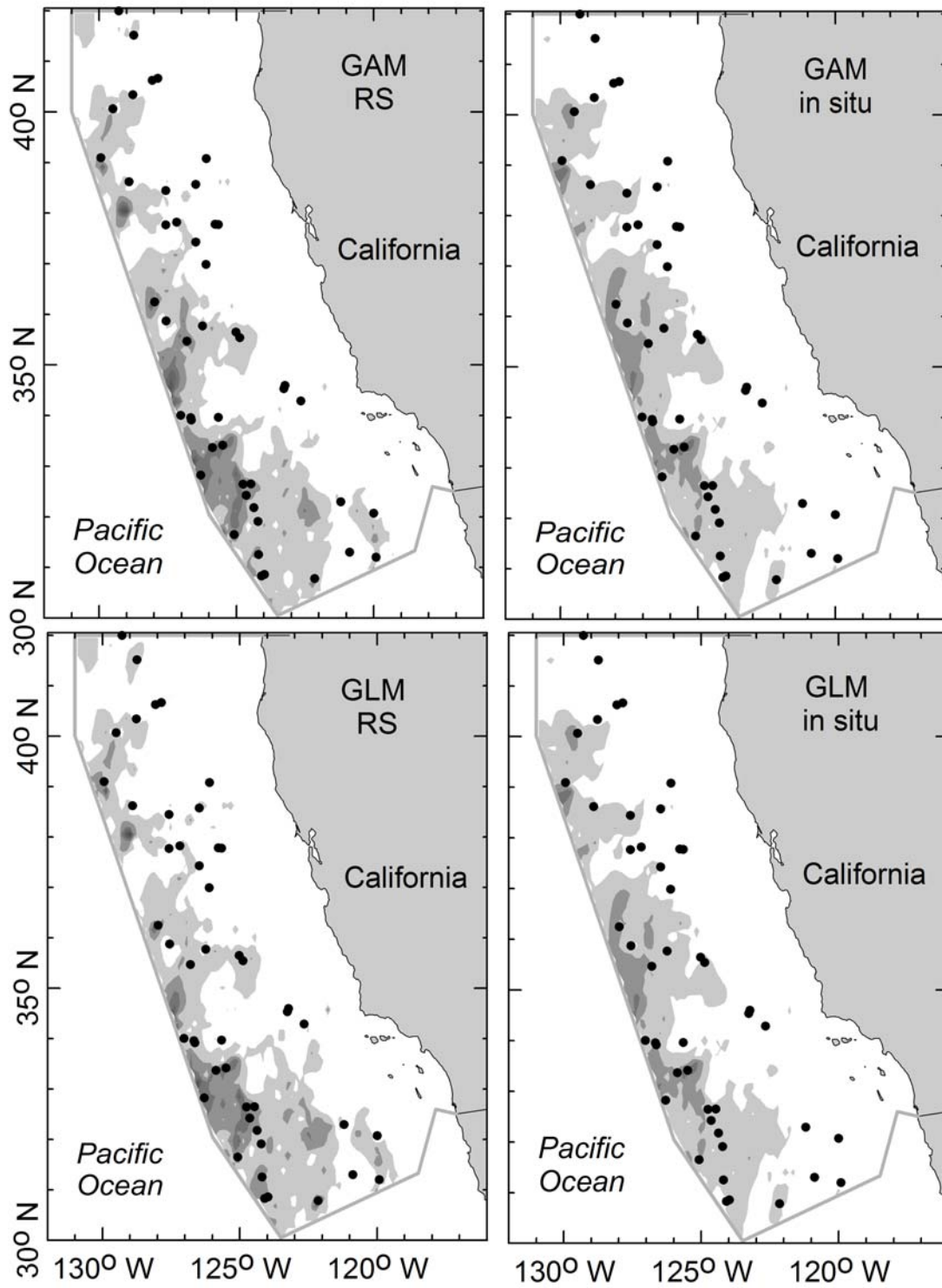
Group size GLM built with *in situ* data



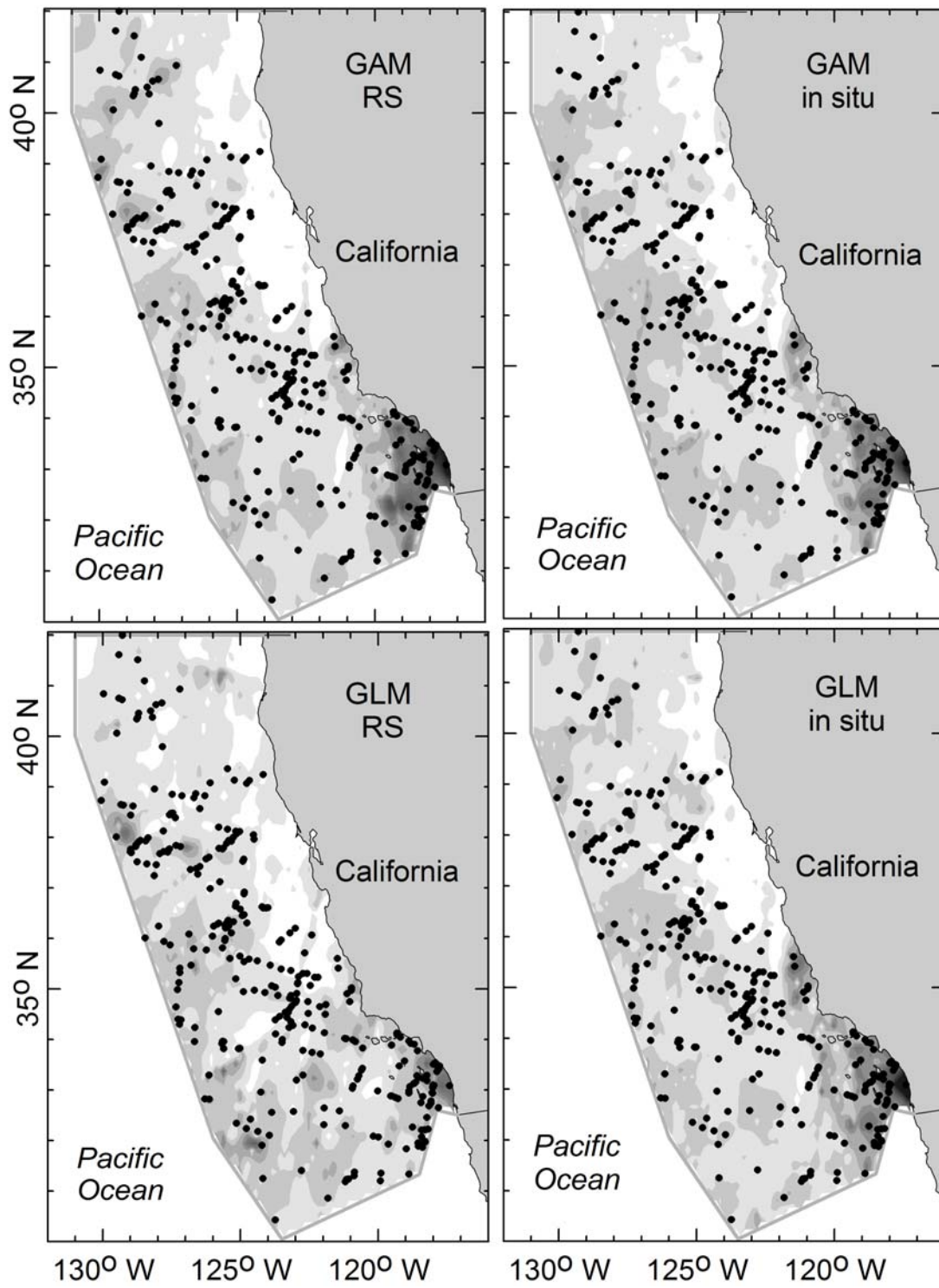
Appendix B

Predicted relative density estimates from the generalized additive and generalized linear models built with remotely sensed and *in situ* data for (a) striped dolphin, (b) short-beaked common dolphin, (c) Risso's dolphin, (d) Pacific white-sided dolphin, (e) northern right whale dolphin, (f) Dall's porpoise, (g) sperm whale, (h) fin whale, (i) blue whale, and (j) humpback whale. Density estimates for each segment were smoothed on a grid resolution of approximately 12 km using inverse distance weighting interpolation to the second power in Surfer software (version 8). The same species-specific relative density scale was used for all models to enable a comparison between data (remotely sensed and *in situ*) and model type (GAM and GLM). Models with obvious outliers were scaled so that differences in predicted densities at lower levels were visible. Black dots show sighting locations.

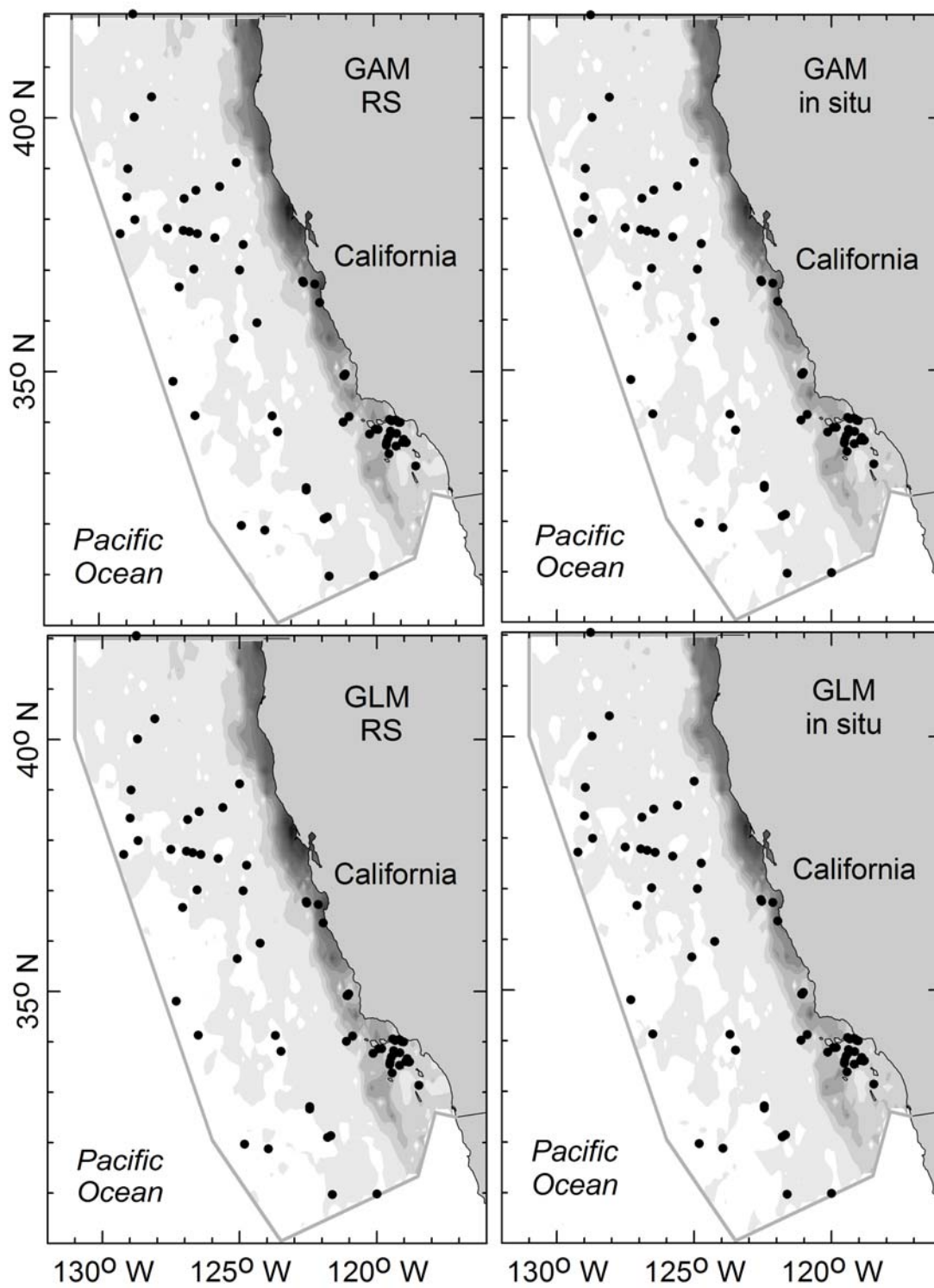
(a) Striped dolphin



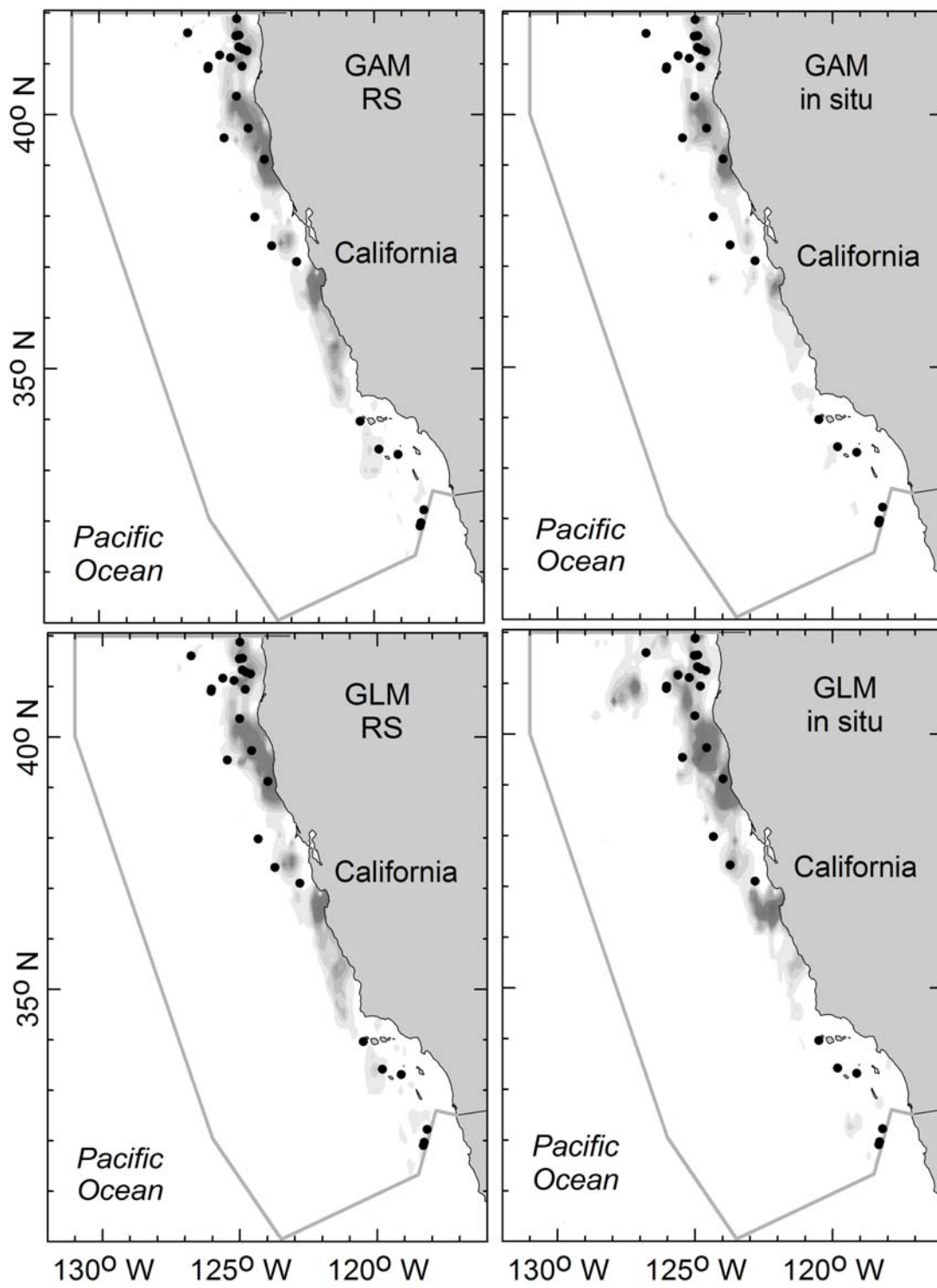
(b) Short-beaked common dolphin



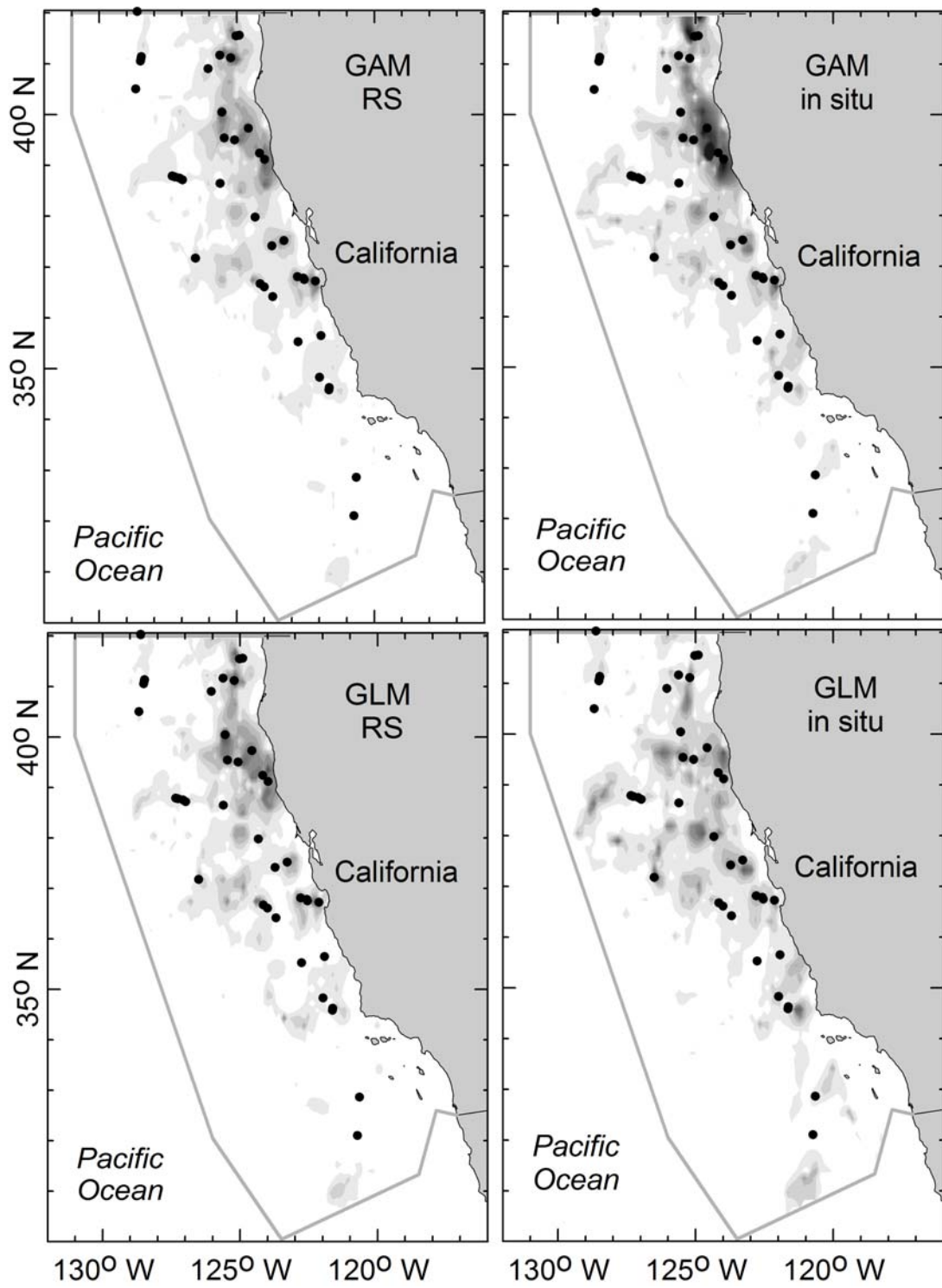
(c) Risso's dolphin



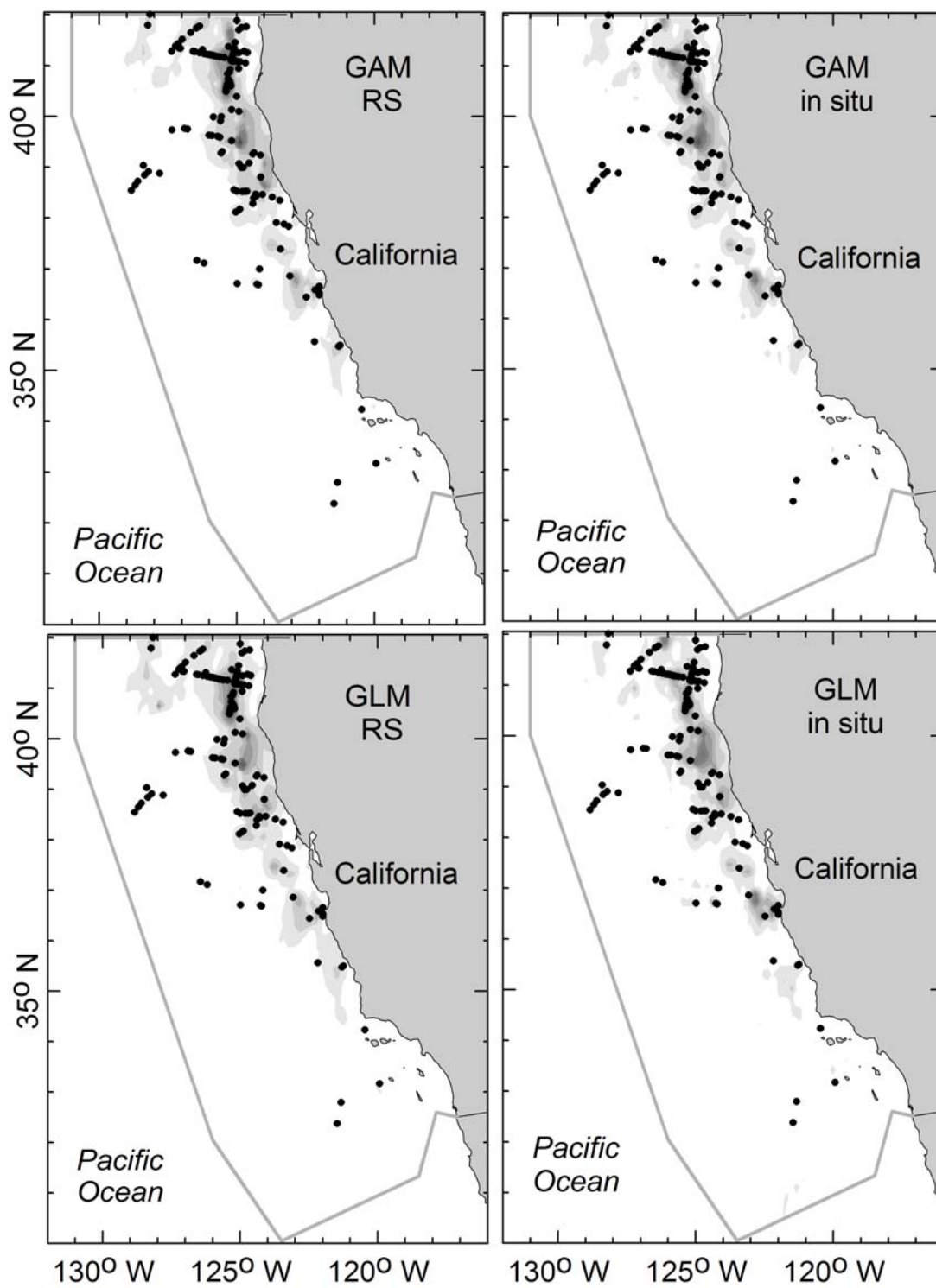
(d) Pacific white-sided dolphin



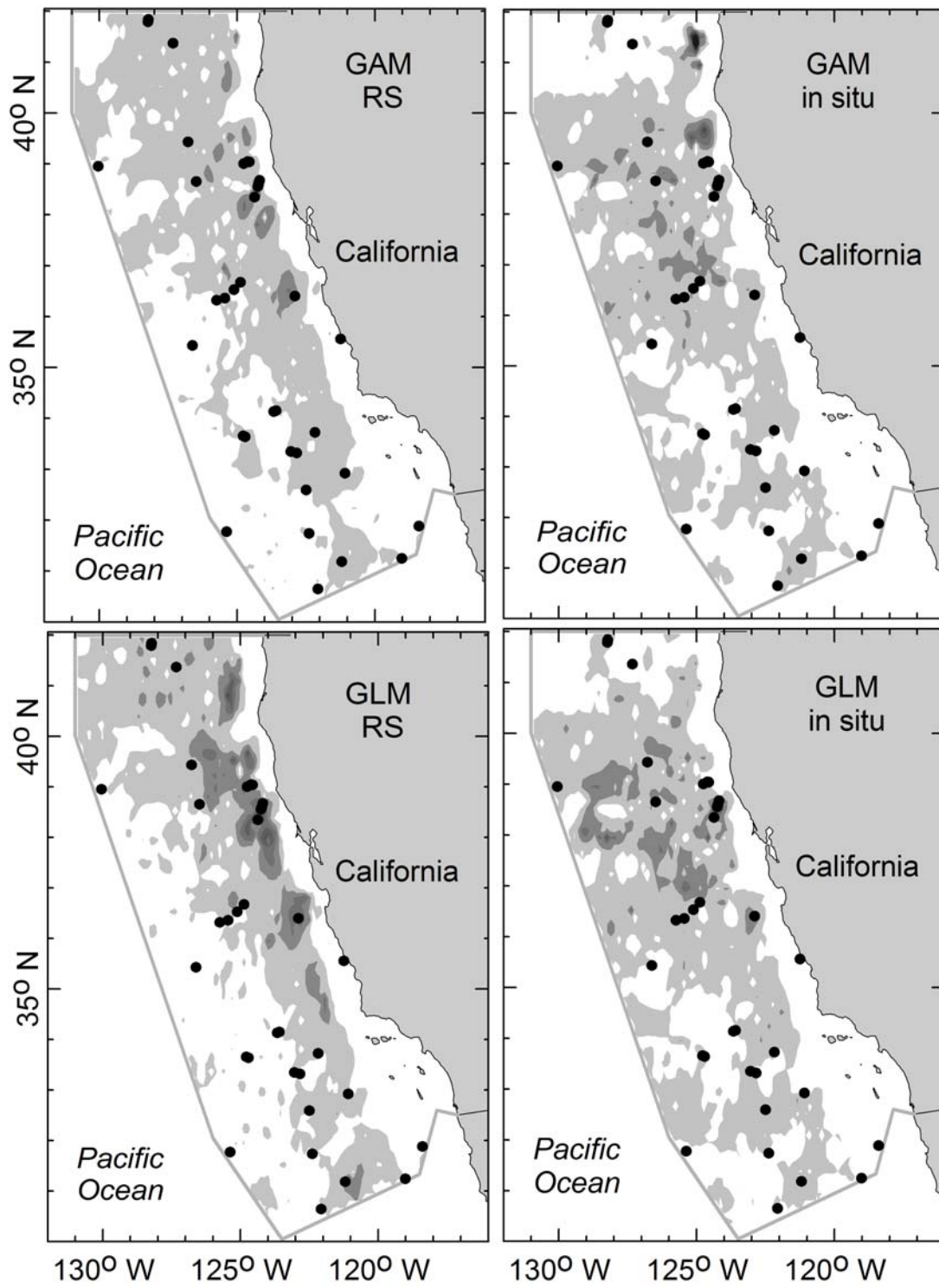
(e) Northern right whale dolphin



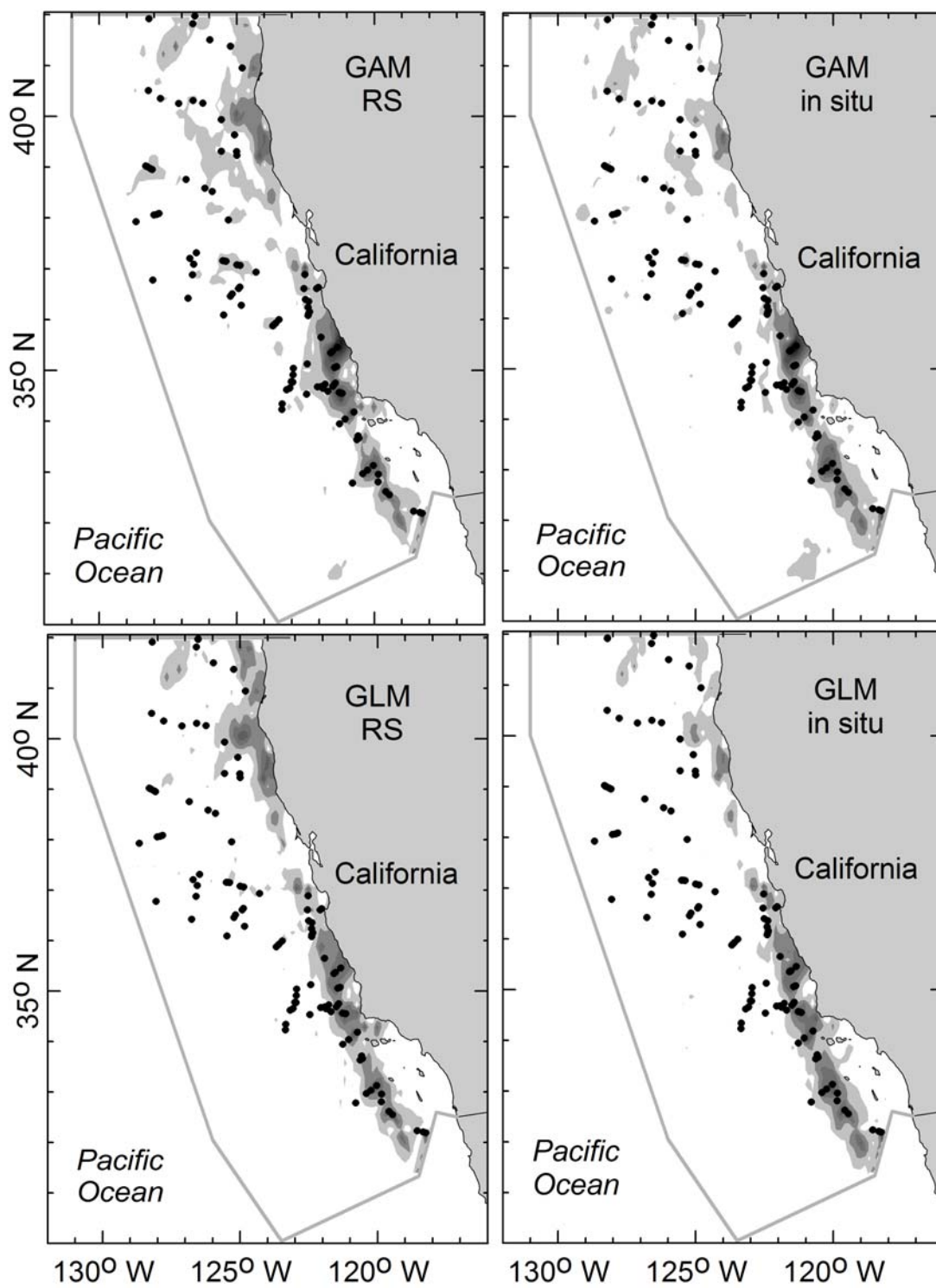
(f) Dall's porpoise



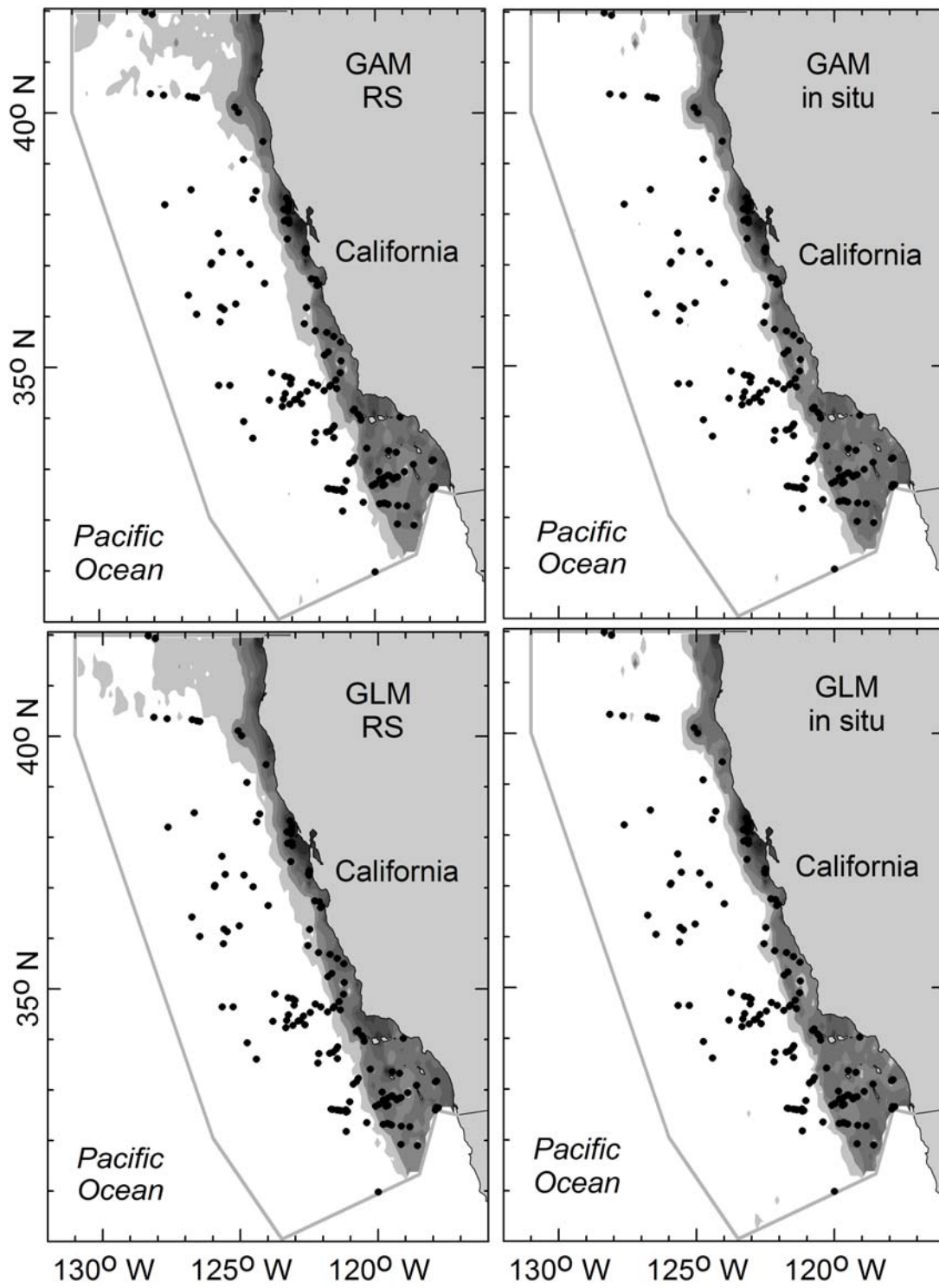
(g) Sperm whale



(h) Fin whale



(i) Blue whale



(j) Humpback whale

